THE DYNAMICS OF HUNTED POPULATIONS OF BRUSHTAIL POSSUMS *TRICHOSURUS VULPECULA* IN TASMANIA: A TECHNIQUE FOR POPULATION ANALYSIS

by

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ABSTRACT

A study of the population dynamics of four hunted populations of the Brushtail Possum *Trichosurus vulpecula* in Tasmania was carried out. Efforts by the management authority, the National Parks and Wildlife Service to monitor and census the species have been hampered by a lack of suitable methods of population assessment. The principal aim of the study was to describe a methodology for timely monitoring of changes in local populations.

The approach taken was distinctive in that the collection of the sample and the analysis were carried out by separate parties. The analysis of the populations was made from material salvaged from commercial hunters in the course of their normal operations. This division of labour reduced the field time required to virtually zero.

The material salvaged from the four populations has been used to give reliable estimates of some population parameters including age structure, sex ratios, natality and recruitment rates. Predictions of the rate and direction of change in the populations were made on the basis of these estimates.

The secondary age ratio was used as an estimate of the rate of recruitment. The effects of hunting could be seen in the high rates of recruitment in these as compared to unhunted populations. The secondary age ratio gave a measure of the intensity of hunting.

Where the estimated production of juveniles was in excess of that needed to maintain the population, characteristics observed in unhunted populations were displayed. These were an age dependent survival between year classes for adults and an adult sex ratio near unity.

For populations where the production of juveniles is insufficient to maintain the population these characteristics are altered. Hunting is unselective with respect to age and sex and when this is intense survival between age classes is approximately constant. Social factors mediate dispersal in juveniles so that the bulk of dispersing individuals are male. A population dependent on immigration to maintain numbers thus tends to recruit males, depressing the proportion of adult females and thus the capacity of the population to produce young. An excess of adult males was found where the production of juveniles was not sufficient to maintain numbers.

The status of the populations can be examined in some detail. Differences between populations are readily apparent and the effects of hunting can be gauged. The results are compatible with those from other studies of the species. The method of assessment allows estimates of changes to be made and provides an appropriate means to spot check the status of local populations of *T. vulpecula*.

TABLE OF CONTENTS

		Page
ACKNOWLEDGEMENTS		i
ABSTRACT		ii
CHAPTER 1	INTRODUCTION	1
CHAPTER 2	BIOLOGY AND ECONOMIC STATUS OF THE BRUSHTAIL POSSUM, *TRICHOSURUS VULPECULA*	7
	2.1 Introduction	7
	2.2 Biology of *Trichosurus vulpecula*	8
	2.2.1 Description and Distribution	8
	2.2.2 Reproduction	9
	2.2.3 Ecology	13
	2.3 Economic Status in Tasmania	16
	2.4 Summary	19
CHAPTER 3	MATERIALS AND METHODS USED	21
	3.1 Introduction	21
	3.2 Salvage of Material	21
	3.3 Collection Areas	26
	3.3.1 Kingston via Nile	26
	3.3.2 Middle Park	28
	3.3.3 Poatina	30
	3.3.4 Maggs Mountain	32
	3.4 Derivation of Age Classes	34
	3.4.1 Adults	34
	3.4.2 Pouch Young	37
	3.5 Summary	41
CHAPTER 4	BREEDING PATTERNS AND PRODUCTION OF YOUNG	42
	4.1 Introduction	42
	4.2 Breeding Parameters	43
	4.2.1 Breeding Season	43
	4.2.2 Incidence of Breeding	49
	4.2.3 Sex Ratios of Pouch Young	51
	4.2.4 Duration of Pouch Life	53
	4.3 Correlations Between Breeding Parameters	55
	4.4 Young Available for Recruitment	57
	4.5 Summary	61
CHAPTER 5	POPULATION STRUCTURE AND DYNAMICS	63
	5.1 Introduction	63
	5.2 Age Structure	64
	5.3 Recruitment and Survival of Adults	66
	5.4 Dispersal and Migration	75
	5.5 Summary	78

TABLE OF CONTENTS (continued)

		Page
CHAPTER 6	EVALUATION OF THE METHOD AND RESULTS FOR MANAGEMENT PURPOSES	80
REFERENCES		91
PERSONAL COMMUNICATIONS		95
APPENDIX A	THE ESTIMATED DAY OF BIRTH FOR ALL POUCH YOUNG AT EACH LOCALITY	96

CHAPTER 1 INTRODUCTION

Human activities have had a profound effect on the abundance of many wildlife species. In Tasmania, European settlement produced changes in land use patterns which appear to have resulted in an increase in both the numbers and the distribution of the Brushtail Possum, *Trichosurus vulpecula*, particularly over the past few decades (Green 1973). This increase has occurred in spite of hunting possums for fur which started in the early days of the colony (Gould 1863) and still continues at a high level in Tasmania (National Parks and Wildlife Service 1984).

Careful monitoring of hunted populations of Brushtail Possums to predict future changes in abundance and to assess the effects of hunting and changing land use is essential. This study describes a practical means of surveying hunted populations of Brushtail Possums so that the response of the populations to this hunting pressure can be effectively monitored. Such a technique is also more widely applicable, particularly in situations where local populations need to be assessed in response to environmental pressures, such as changing land use.

The responsibility for conservation of wildlife in Tasmania lies with the National Parks and Wildlife Service. In this State, three species of marsupials are commercially exploited: the Bennetts Wallaby (*Macropus rufogriseus*), the Tasmanian Pademelon (*Thylogale billardierii*), and the Brushtail Possum (*Trichosurus vulpecula*). All three species are timid, cryptic, and essentially nocturnal; census methods potentially

suitable for these sorts of animals are not well developed.

The National Parks and Wildlife Service collects information to provide indices of abundance for Brushtail Possums. It collects statistics concerned with the fur trade, carries out quarterly counts of animals killed on roads and conducts an annual spotlight survey. The indices obtained from this information are outlined briefly below (from Johnson 1977).

1. Catch/effort Ratio: Brushtail Possums are shot under a licensing system and royalties are payable by dealers on marketable skins. An approximation of catch/effort ratio is made as the number of royalties paid per permit. This is subject to error in that royalties are not paid on all skins and indications are (Coulson and Heron 1981) that in some area as few as 40% of the animals shot are skinned. The effort hunters are willing to put in to take their catch is affected by factors other than the abundance of possums. Obvious influences would be skin prices and weather conditions.

2. Road Kill Survey: It is assumed that the frequency of road kills is related to the density of the living population. Variation in traffic intensity is corrected against traffic flow figures from the Department of Main Roads. The index used is the number of possums killed per 1000 vehicles per transect. Because sample sizes are small, the random error is large. Most transects are more than 100 km long and pass through several vegetation types so regional and habitat differences are masked.

3. Annual Spotlight Survey: This is carried out in roaded parts of the state over 50 standard transects, each 10 km long, from a slowly moving vehicle, when visibility is good, and in the same month of the year. It is invalid to compare relative densities obtained from different survey areas unless the conditions for sighting the animals are the same in each place.

The data available to monitor the populations of Brushtail Possums in Tasmania provides indicators of trends in the population. Such indicators are known as indices and can provide only a rough guide to changes within populations.

The collection of reliable census information, whether the aim is conservation, pest control, or commercial exploitation, is the first step in scientific management of a species. The methods listed above are those currently used to monitor the populations of Brushtail Possums in Tasmania. All are subject to large and unquantifiable error so that accurate censusing of the populations is not carried out. None of them have been used to describe the population in terms of age structure, sex ratio, natality or mortality. Existing methods for obtaining this information are expensive in terms of time and resources so that while this information is highly desirable for the management of exploited populations, it is not practicable for the managing authority, the National Parks and Wildlife Service, to obtain it.

The methods used to monitor populations of the Brushtail Possum in Tasmania do not provide information on those parameters most important to predicting changes in the population. While this information gap has long been recognised by the National Parks and Wildlife Service (Johnson 1977; Coulson and Heron 1981) a more cost effective method for obtaining the pertinent information has not yet been made available.

As part of an on-going programme of building up a reference collection of samples from native mammals the Queen Victoria Museum, Launceston, arranged for the salvage of material from commercial Brush-tail Possum shooters during the winter of 1979. This material was collected, cleaned and catalogued by museum staff so that a reference collection from some hunted populations of Brushtail Possums is available for examination. This material forms the basis of the present study.

The salvaged material, consisting of a series of skulls and pouch young taken from four separate populations, has been examined with the object of determining the structure and dynamics of the parent populations.

A detailed description of the sampling method and the collection details follows in Chapter 3, it is out-lined briefly here. The museum enlisted the co-operation of four licence holders shooting over four widely separated areas of the state. They agreed to collect the skulls and pouch young from all and only those Brushtail Possums shot by them during the open season of 1979. Skulls from males and females were collected separately. The skulls and pouch young were picked up fortnightly by museum staff during the season. At each locality animals were spotlighted and shot in areas adjacent to, or in forest or woodland. Between the sites, there were differences in the main tree species present, the type of forest or woodland, the terrain and the main types of land use.

The aim of this study is to present a technique for assessing the dynamics of local populations of Brushtail Possums that can be incorporated

into existing programmes for monitoring possum populations. The salvaged material has been analysed and information on the age structure, natality and sex ratios of the studied populations has been derived. Comparison of successive sets of this information for local populations would allow rapid assessment of both the rate and the direction of changes, if any, in the structure of the populations under the land use and hunting regime the particular population is subject to. The estimates derived are standard ones used universally in examining the structure and the dynamics of populations. Because of this the data analysis is in a form that can be directly compared with data from other studies of the species reported in the literature.

The major objectives of the study are two-fold:

1. to present an analysis of the material salvaged from hunted populations of Brushtail Possums to demonstrate the effectiveness of this method of population analysis;
2. to compare the indices of population structure found in these hunted populations with those reported for other populations of Brushtail Possums in different habitats and under different management regimes.

The technique has been developed solely on the basis of a laboratory analysis of salvaged material. This is partly because of the limited time that was available and partly to work within the constraints that the National Parks and Wildlife Service would be under if applying the method. The brevity of the field and laboratory work sets this report apart from more detailed long-term studies of the Brushtail Possum but does not detract from its validity or the analysis of population structure. The advantage of this technique is that a number of standard estimates of population structure and dynamics can be derived

quickly and without the need for lengthy periods in the field.

The body of the thesis is divided into five parts. A review of the biology of the Brushtail Possum, *Trichosurus vulpecula*, with an emphasis on population structure and dynamics is followed by a discussion of the economic importance of the species in Chapter 2. A description of the methods used in collecting and analysing the samples is given in Chapter 3, together with a brief description of each collection area. Population structure is divided into two sections. Firstly, in Chapter 4, the breeding patterns found in the studied populations are analysed and compared with those found in other populations. Secondly, in Chapter 5, the age structure and sex ratio of the adult populations are examined. Finally, the integration of this method of population analysis into the programme of monitoring the species that has been adopted by the National Parks and Wildlife Service is discussed in Chapter 6. The potential benefits for using this system of assessment to either supplement or replace some of the present methods used to census the Brushtail Possum in Tasmania are given in this final chapter.

CHAPTER 2 BIOLOGY AND ECONOMIC STATUS OF THE BRUSHTAIL POSSUM, *TRICHOSURUS VULPECULA*

2.1 INTRODUCTION

This chapter reviews current biological knowledge of the Brushtail Possum, *Trichosurus vulpecula*, both in Australia and New Zealand. *Trichosurus vulpecula* has been the subject of a considerable amount of research to the extent that it is one of the best known species of marsupials. Bolliger (1940) described the virtues of this readily obtainable and easily maintained species as an experimental animal. The species is discussed here mainly in terms of its population structure and dynamics, concentrating more on the traits of populations rather than on those of individual animals.

Many of the studies investigating the population structure and ecology of *T. vulpecula* have been carried out in widely separated parts of its range and in a variety of habitats. These diverse studies allow a composite picture of the patterns of response by populations in different habitats to be built up.

Much of the information on the ecology of *T. vulpecula* comes from studies relating to its role as a pest species. Most of this work has been done in New Zealand where it was introduced around the middle of last century and has so successfully adapted to the local conditions that it has become a major pest having a profound effect on the native forests (Pracy and Kean 1949; Pracy 1974).

The economic status of Brushtail Possums in Tasmania is discussed with particular reference to the long-term hunting pressure the species

has sustained. Tasmania is unique among Australian states in allowing the commercial exploitation of the species as a fur bearer.

2.2 BIOLOGY OF *TRICHOSURUS VULPECULA*

2.2.1 Description and Distribution

The Brushtail Possum, *Trichosurus vulpecula* (Kerr 1792), is a herbivorous, diprotodont, syndactylous marsupial belonging to the Family Phalangeridae which includes the genera *Trichosurus*, *Wyulda* and *Phalanger*, the large possums and the cuscuses, a group of primarily arboreal animals.

The Brushtail Possum is one of the most familiar of Australia's mammals, well adapted to arboreal life with large hands and feet giving it a powerful grasp, and with a prehensile tail.

Adult body weights range from around 1 kg in northern Australia to more than 4 kg in Tasmania (Tyndale-Biscoe 1973). A variety of colour phases have been noted, some with regional distribution. This variation has led to a number of species and sub-species being recognised; current authorities (Ride 1970; Kirsch and Calaby 1977) place the Tasmanian Brushtail Possum *T. fuliginosus* (Ogilby 1831) within *T. vulpecula*.

Tasmanian possums show two distinct colour phases, "black" and "grey". The "black" form is associated with the denser vegetation and higher rainfall of closed-forest* and tall open forest; the "grey" form

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* Vegetation terms used in this report are according to Specht (1973). The following table compares the classification of vegetation by Specht with some other commonly used terms.

Specht's Term	Equivalent Term
Closed-forest	Rainforest
Tall open-forest	Wet sclerophyll forest
Open-forest	Dry sclerophyll forest

predominates in drier areas of open-forest and woodlands (Guiler and Banks 1958). In addition, there is a rare "cream" colour phase in Tasmania and albinos have been reported (Hocking 1981).

The Brushtail Possum has an extensive distribution through the wooded parts of the Australian mainland and occurs throughout most of Tasmania (Ride 1970). Within this range, it is found in a variety of habitats from suburban gardens to closed-forest and woodland communities. The most important habitats are open-forest and woodland. Partial clearing of denser forests favours an increase in numbers (Frith 1979). Possums were first released to the wild in New Zealand in 1838, where they have so successfully adapted to the local conditions that they have become a serious economic pest in many localities (Pracy 1974).

In Tasmania, the Brushtail Possum is found in most habitats, having been recorded from agricultural lands, open and tall-open forests, coastal heaths and moorland. It has not been found in closed-forest except where the forest has been opened up by roads and logging tracks (Guiler 1965). It has not been recorded from the tall-open forests in the lower Gordon Valley (Hocking *et al.* 1978) possibly because migration into the area has been impeded by the wide distribution of closed-forest and sedgeland in the region.

On the Australian mainland, the Mountain Possum (*T. caninus*) is found in closed and tall-open forest with *T. vulpecula* found in open-forest and woodland (Calaby 1966). The Mountain Possum is not present in Tasmania, nor has it been introduced to New Zealand; in the absence of this species, *T. vulpecula* has occupied the wetter forests that are occupied by *T. caninus* on the mainland.

2.2.2 Reproduction

Trichosurus vulpecula is a monovular, polyoestrous marsupial, in which the oestrous cycle is approximately 26 days and the

gestation period 17.5 days. After parturition, lactation inhibits oestrus but, on removal of a suckling pouch young, females come into oestrus within 8 days (Pilton and Sharman 1962).

The main season of births in all populations examined is during the autumn months of April, May and June. Crawley (1973), Hocking (1981) and How (1981) found that births occurred only in the autumn months for three widely separated populations, in New Zealand, southern Tasmania and northern New South Wales respectively. Most other studies (Bolliger 1942; Dunnett 1956, 1964; Lyne and Verhagen 1957; Owen 1964; Smith *et al.* 1969) record some level of spring breeding in addition to the main autumn period, or a low level of breeding over most of the year but with a pronounced autumn peak (Tyndale-Biscoe 1955; Pilton and Sharman 1962). *T. vulpecula* has been bred in captivity; breeding records of the London Zoo show no evidence of seasonal breeding and that at least two litters could be produced each year (Zuckerman reported in Collins 1973).

The contribution made by spring births to the total reproductive output of a population varies from 30% for possums living in woodland near Canberra (Dunnet 1964) to near zero for populations living in closed-forest in New Zealand (Crawley 1973) and tall-open forest in southern Tasmania (Hocking 1981). Variation in spring breeding between different habitats

in the same area, e.g. 3% and 15% in two different aged pine plantations 10 km apart at Tokaroa, New Zealand, show the importance of local conditions on the expression of the spring breeding peak (Brockie *et al.* 1979). Populations with high levels of spring breeding have many double breeders (the same animal producing young in autumn and again the following spring), showing that spring breeding is not solely a compensatory opportunity for animals that were unsuccessful breeders in the autumn season (Brockie *et al.* 1979).

There are two teats in the pouch, but multiple births in the wild are rare, females normally giving birth to only one young at a time. Kean (1971) found that, of 8000 females carrying young, only one had twins. One female with twins was found in the course of an examination of around 200 female possums with pouch young from Sydney suburban populations. This restriction on multiple births has been found to relax with captive breeders. Zuckerman (reported in Collins 1973) found that, of 60 births in the London Zoo, 6 resulted in twins and one in triplets.

T. vulpecula females have been found to first bear young at either one year of age (Tyndale-Biscoe 1955; Dunnet 1964; How 1981; Smith *et al.* 1969) or two years of age (Gilmore 1969; Crawley 1973; Hocking 1981). The proportion of females first breeding at a given age varies between populations. How (1981), working on the Clouds Creek population in northern New South Wales, found all one-year-old females breeding; by contrast, Crawley (1973) found that most females in the Orongorongo Valley did not give birth till they were at least two years of age and some were three or four years old before their first parturition.

More than 80% of reproductively mature females give birth each autumn in most populations in Australia and New Zealand (Brockie *et al.* 1979). In southern Tasmania, Hocking's (1981) study found that, for the populations he examined, the percentage of females giving birth each autumn ranged

between 80 and 100% and that the percentage of females giving birth in each population was related to the habitat type. The variation found among the populations in southern Tasmania encompasses most of that found in other studies across the range of the species (Hocking 1981).

Young possums are dependent on their mothers for at least the first six months of life (Dunnet 1964). First emergence from the pouch has been recorded as early as 121 days (Dunnet 1956) with weaning at around 200 days. In the tall-open forests of southern Tasmania, there is a more protracted period of development. First emergence from the pouch is at around 180 days with weaning at around 225 days (Hocking 1981). Comparison of the growth rates of pouch young from the different populations show that this delay in emergence is not associated with slower growth of the pouch young but that young are weaned at a larger stage (Hocking 1981). Kean (1971) reports some New Zealand populations with very long periods of dependence, young in some populations being suckled for at least 240 days. Kean suggested that this long period of maternal dependence is found in populations with low reproductive rates and where food resources are limiting.

Most studies of *T. vulpecula* indicate a survival rate of dependent young of more than 90% (Tyndale-Biscoe 1955; Dunnet 1964; How 1972; Clout 1977). Hocking (1981), in a study of several populations in southern Tasmania, found an overall survival rate of 77% for dependent young, the survival rate decreasing with the age of the habitat, in this case, the period since a regeneration burn.

The timing of the main autumn breeding period varies from place to place and from year to year. Data from a number of studies suggests that there are some consistent differences related to habitat (Brockie *et al.* 1979). Populations with early median dates of birth have a high

reproductive output in that females first breed at a younger age, there is a high incidence of double breeding, and the proportion of females giving birth is higher than in populations with late median dates of birth (Brockie *et al.* 1979). Estimates can be made of the productivity of different populations based on the combined effect of these variations in reproductive effort. These range from 1.4 young per female per year at Canberra (Dunnet 1964) to 0.36 young per female per year in Orongorongo Valley. Thus, minor variations in various measures of reproductive effort can combine to significantly affect the productivity of a population (Brockie *et al.* 1979).

2.2.3 Ecology

The primary habitat of the Brushtail Possum is in the moderate climate of the woodlands and open *Eucalyptus* forests of Australia. On the mainland, the Mountain Possum (*T. caninus*) is found in the tall-open forests and the closed-forests of south-east Australia and the distribution of the two congeneric species overlaps very little (How 1974). *T. caninus* is absent from Tasmania and New Zealand and, in these places, *T. vulpecula* lives in the tall-open forests that are on the mainland occupied by its congener.

In the natural habitat of grassy and shrubby *Eucalyptus* forests in mainland Australia, populations reach densities of around 2 possums per hectare and exhibit little fluctuation from one year to the next (Winter 1976). It has been suggested that the occurrence of toxic secondary compounds in *Eucalyptus* limits the amount of *Eucalyptus* leaves that can be consumed and that possums have to consume non-*Eucalyptus* species in order to subsist. It is the availability of these other foods rather than the abundance of the major food item (*Eucalyptus* leaves) that limits the size of the possum population (Freeland and Winter 1975).

When *T. vulpecula* was introduced into New Zealand, numbers rose rapidly, frequently reaching densities in excess of 30 per hectare (Batchelor *et al.* 1967). In Australia, where exotic pasture species are available at forest margins, densities of up to 8 possums per hectare have been found (Johnson 1977). In line with the above hypothesis, it would seem that, where palatable food plants without toxic secondary compounds are readily available, there is a population explosion and a very high density of possums per hectare is found.

In a high productivity population such as that near Canberra studied by Dunnet (1964), the adult population could potentially be replaced if each female bred for only two years. In the lowest productivity population yet described (Orogorongo Valley), each female would need to breed for six years to potentially replace the adult population, yet the density of possums in the Orogorongo population is up to 14 per hectare and that of the Canberra population is around 2 per hectare. Thus, in a stable population, the realized fertility must be seriously reduced.

For a mammal of the size of a possum with a high reproductive potential, it could be expected that population turnover would be rapid and life expectancy relatively short. This is not found to be so, most capture/release studies having found that the locations examined support resident populations of adults that remain through the course of the study. Long-term studies have found animals routinely living in excess of 8 years and Crawley (1970) reports a female of 12+ years carrying a pouch young. Records show individual *T. vulpecula* living for up to 12 years in captivity (Collins 1973). Population turnover is low, and life expectancy for adults is long.

Adult *T. vulpecula* tend to be solitary, rather sedentary animals making only occasional sallies beyond the perimeter of an established home range. The movement patterns of *T. vulpecula* have been studied in a variety of habitats. These include native forest in Australia (Dunnet

1964; Winter 1970, 1976; Hocking 1981) and New Zealand (Tyndale-Biscoe 1955; Crawley 1973, Jolly 1976), and exotic pine plantations (How 1972; Clout 1977). Home range sizesrevealed in these studies were consistently larger for males than for females, and were characterised by temporal stability with little seasonal variation. There were great differences in the absolute size of the home range in different habitats (from 0.81 ha to 9.0 ha for males) but the dispersion and the movement patterns revealed were essentially similar in all. In heterogeneous habitats, such as pasture-scrub mosaics, possums move out of the forest to feed on the pasture, an essentially linear expansion of the range (Jolly 1976). Home range size has been related to the quality of the habitat in a number of species, and this appears to be the case with *T. vulpecula* (Hocking 1981).

Home ranges overlap (Dunnet 1964; Winter 1976) but territorial behaviour is not marked and home ranges are not aggressively defended (Winter 1976). Encounters between adults of either sex are usually mild, the animals tending to avoid direct contact. Avoidance behaviour between males and females is only reduced at oestrus. There is no pattern of mutual grooming, the only long-term contact between individuals is that between a mother and her dependent young. This close contact gradually declines and, when the juvenile is about 9 months of age, the mother shows increasing antagonism towards it, usually succeeding in driving it from the natal area.

Social and behavioural factors thus operate to keep adult possums separated from each other and to keep the population dispersed. The pattern of survival in *T. vulpecula* is characterised by a rate of disappearance of juveniles that is both high and variable (Hocking 1981). Survival rates outside this time are high both for pouch young and adults. The importance of juvenile survival in the population dynamics of the species is recognised by How (1972) who considered it to be the main factor in

determining the rate of recruitment to the adult population.

The period of juvenile life co-incides with the major period of dispersal in *T. vulpecula* (Dunnet 1964; How 1981; Hocking 1981). Dispersal reflects the inability of the dispersing individuals to establish home ranges in fully occupied habitat. These individuals are seen as a surplus to the population that will perish unless they find unoccupied habitat. If mortality is imposed on the adult population, juvenile survival is enhanced and the proportion of young animals in the population increases (Tyndale-Biscoe 1973).

There are social mechanisms maintaining the dispersion of possums through their habitat. These mechanisms prevent juveniles from establishing themselves in an area already occupied by resident adults and, unless unoccupied habitat is available, they will perish. In this sense, the population is self-regulating with density determining survival.

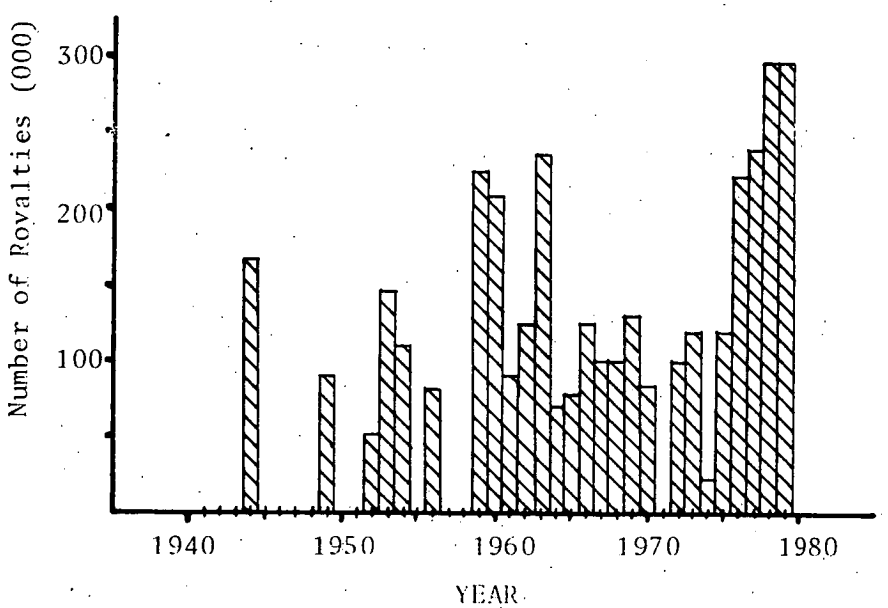
2.3 ECONOMIC STATUS IN TASMANIA

Trichosurus vulpecula is of considerable economic importance in Tasmania. Marsupials, including the Brushtail Possum, have been harvested for fur since the European settlement of Australia (Gould 1863). Today, the Brushtail Possum is exploited as a fur bearer only in Tasmania and in New Zealand where it was introduced last century with the expressed intention of starting a fur industry (Wodzicki 1950).

In Tasmania, the harvest of possum pelts has developed into a substantial industry, worth $2 million to the state in 1979. Between 1923 and 1955, the catch varied from 50 000 to 160 000 during the annual open season. Guiler (1957) found no evidence to suggest that the possums were over-exploited by hunting during this period. Numbers harvested in recent years have been greater, approximately 300 000 in 1979 (Mooney 1980). Evidence (Green 1973) suggests that the species has increased in

both numbers and distribution during this period. The number of royalties paid on Brushtail Possum skins per annum is the only long-term indicator of the hunting mortality sustained by the species in Tasmania. The number of royalties paid on skins sold is shown below (Figure 1).

FIGURE 2.1 Royalties paid annually on skins from Brushtail Possums in Tasmania from 1940-1979 (figures from Coulson and Heron 1981).



In New Zealand, the possum fur industry has become an increasingly important provider of both local employment and export earnings. In 1979/80, the export of 3.1 million skins was worth over $23 million in foreign exchange (Clout and Barlow 1982).

The Brushtail Possum has long been regarded as a serious pest in forestry and agriculture, especially in New Zealand where concern over the damage done to crops and native forests led to its being declared a noxious species in 1947. Serious damage to exotic trees in Australia was reported as long ago as 1919 (Gill in Wodzicki 1950).

Damage to exotic pine plantations has been attributed to *T. vulpecula* in both Australia and New Zealand (How 1972; Clout 1977; Pracy 1974). In Australia, damage to native forest appears restricted to areas of recently regenerated forest (Johnson 1978; Mollison 1960). Where cleared agricultural land forms a mosaic with wooded land, possums have been found to move out to feed on pastures at night, seeking refuge in the forest by day (Johnson 1977; Jolly 1980).

Extensive browsing damage by native mammals and the rabbit occurs in Tasmanian forest areas. *T. vulpecula* has been named as the culprit species causing damage to six-year-old *Pinus radiata* plantations at Mt Lloyd, Tasmania (Johnson 1978). *P. radiata* has been eaten in significant proportions by *T. vulpecula* in New Zealand (Clout in Statham 1983). On the mainland, *T. caninus* is responsible for most possum damage to exotic pines (Barnett *et al.* 1977); *T. vulpecula* is not usually found in the plantations. A recent study of browsing damage to *P. radiata* plantations in Tasmania concluded that *T. vulpecula*, together with *Thylogale billardierii* and the rabbit, was responsible for less than 3% of the total damage, the main culprit being *Macropus rufogriseus* (Statham 1983).

T. vulpecula was thought to be partially responsible for browsing damage to regenerating *Eucalyptus regnans* in the Florentine Valley (Cremer 1969; Mollison 1960). Gilbert (1961) considered this damage minor in comparison with that done by *Macropus rufogriseus* and *Thylogale billardierii*. Statham (1983), investigating browsing damage to *E. delegatensis* regeneration in the Mersey Valley, found *T. vulpecula* was a minor culprit. These results are consistent with the study of the feeding patterns of *T. vulpecula* made by Freeland and Winter (1975) in which they found mature *Eucalyptus* leaves to be a preferred food item, and that ground foraging was confined mainly to non-*Eucalypt* species.

The exact component of browsing damage to exotic forests and regenerating *Eucalyptus* sp. done by *T. vulpecula* in Tasmania remains uncertain.

The indications are that it is very minor in comparison with that done by other browsing species, unlike the situation in New Zealand where the damage done to native and exotic forests by *T. vulpecula* has been immense.

In Tasmania, the Brushtail Possum is not considered a serious pest by agriculturalists, although they are occasionally a nuisance in orchards (Gregory, personal communication). Damage done to crops and pastures by possums is seen as negligible compared with that done by wallabies and rabbits. During 1979, only 6% of the Crop Protection Permits issued by the National Parks and Wildlife Service were for the control of possums. It is estimated that, during the same year, more than 400 000 possums were taken by hunters (Coulson and Heron 1981). This vigorous hunting is undoubtedly likely to reduce numbers sufficiently to control crop damage in most cases.

In Tasmania the main cause of mortality to possum populations is hunting for fur. The National Parks and Wildlife Service has the responsibility for regulating this hunting pressure so that the numbers of Brushtail Possums are maintained. The numbers of possums that can be safely harvested from a population is geared to the productivity of the population. Thus a close monitoring of the hunted populations is necessary, particularly populations such as those studied by Hocking with a low potential for increase, to reliably estimate the long-term hunting pressure that the species can stand in Tasmania.

Tourism is an important industry in Tasmania, contributing $245 million, or 7% of the state's GDP, in 1981 (Bureau of Industry Economics 1984). The main reasons given by overseas tourists for choosing Australia as a destination are "landscape, climate and wildlife" (Patterson, personal communication). Adverse publicity overseas concerning the commercial exploitation of native fauna could have a detrimental

effect on future income from this industry.

2.4 SUMMARY

The Brushtail Possum is a common, widely distributed marsupial found across most of Tasmania. There are minor variations in the breeding patterns and population structures found across the range of the species. These minor variations tend to act together to produce populations with vastly different capacities to increase in numbers (Brockie *et al.* 1979).

The only major study of *T. vulpecula* in Tasmania (Hocking 1981) found that the Tasmanian populations examined fell within the range of variation already observed for the species. These were populations living in the tall-open forests of southern Tasmania and considerable cross-correlation among the different measures of breeding performance was found. Overall the measures of breeding performance examined suggested a population with a low potential for increase.

The major period of high mortality in undisturbed Brushtail Possum populations is during the dispersal phase of the juveniles where those individuals unable to establish a territory perish. Adult mortality in these populations is low. In Tasmania, Brushtail Possums are hunted for fur and this is a major cause of death for adults. The responsibility for monitoring Brushtail Possum populations so that numbers are maintained at a desired level rests with the Tasmanian National Parks and Wildlife Service.

CHAPTER 3 MATERIALS AND METHODS USED

3.1 INTRODUCTION

For many years, in Tasmania the Brushtail Possum was subject to an open season during the winter months when animals could be shot, snared, or trapped under licence for their commercially valuable skins. In response to public outcry over the indiscriminate killing of native animals, the open season was replaced in 1974 with a system of "special permits". These are issued by the National Parks and Wildlife Service to an individual for the taking of possums by shooting only, and then only in areas where the Service considers their numbers and browsing habits are causing damage.

A restricted number of "special permits" is issued each year; the number is determined by the National Parks and Wildlife Service on its estimate of the level of hunting pressure the Brushtail Possum can sustain. Since 1974, royalties have been paid on between 200 000 and 300 000 pssoum skins per annum. It is estimated that an average of 73% of possums shot have saleable skins so that the number of royalties paid represents about three-quarters of the total number shot in a season (National Parks and Wildlife Service, unpublished report 1984). In 1979, 2640 permits were issued, resulting in the payment of royalties on 295 000 skins (Mooney 1980).

Skulls and pouch young salvaged by hunters from commercially exploited populations of Brushtail Possums are held as a reference collection at the Queen Victoria Museum, Launceston.

3.2 SALVAGE OF MATERIAL

During the winter of 1979, the Queen Victoria Museum, Launceston, took the opportunity to salvage some of the pouch young and skulls of animals shot under permit. Before the season opened, the curator of zoology at the museum arranged with four separate permit holders for each of them to collect the heads and pouch young from all and only those possums shot by them under their respective permits. Each hunter collected material from a different area so the collection is made up of four series of skulls and pouch young from separate localities.

After skinning the heads were removed and threaded on wire. Heads from males were collected separately from those of females. Juvenile, and obviously "rumpy" possums, are not usually skinned even if shot, but the skulls from these animals are included in the collection. "Rumpiness" is a local term used to describe a condition where fur is coming away from the skin at the base of the tail due to mite infestation (Munday 1978). In total, the heads of 624 males and the heads of 520 females were collected. The pouch of each female shot was examined and any pouch young found was removed and stored in 4% buffered formalin. A total of 397 pouch young were collected.

TABLE 3.1 Material collected and dates of collection trips for Brushtail Possum material during 1979

Locality	Material Collected	Date of Collection Trip 18/6	2/7	16/7	29/7	13/8	26/8	All Trips
'Kingston' via Nile	Total skulls	31	47	103	38	50	58	327
	Male skulls	15	28	70	21	32	31	197
	Female skulls	16	19	33	17	18	27	130
	Pouch young	10	19	20	12	17	22	100
'Middle Park'	Total skulls	92	103	79	61	36	28	399
	Male skulls	48	62	39	28	21	17	215
	Female skulls	44	41	40	33	15	11	184
	Pouch young	35	36	35	33	12	11	162
Poatina	Total skulls	74	21	40	27	61	91	314
	Male skulls	38	10	22	11	29	50	160
	Female skulls	36	11	18	16	32	41	154
	Pouch young	21	4	15	7	26	35	108
Maggs Mountain	Total skulls					35	41	76
	Male skulls					19	21	40
	Female skulls					16	20	36
	Pouch young					8	19	27
All sites	Total skulls	197	171	222	126	182	218	1116
	Male skulls	101	100	131	60	101	119	612
	Female skulls	96	71	91	66	81	99	504
	Pouch young	66	59	70	52	63	87	397

This material was picked up and recorded by museum staff every fortnight during the shooting season. The date of death was assumed to be seven days before the date of collection by museum staff thus giving the date of death with an accuracy of up to 7 days. The material picked up on each collection trip is shown in Table 3.1.

The heads of the possums were deep frozen until cleaned. The Queen Victoria Museum has a colony of dermestid beetles which was used to clean perishable material from the skulls. As possums are usually shot in the head or neck region to avoid skin damage many of the skulls collected were badly shattered. Only those skulls with minimal damage were registered as museum cabinet specimens, those more extensively damaged being discarded after counting. A total of 381 skulls were kept as museum specimens. The proportion kept from each locality is shown in Table 3.2.

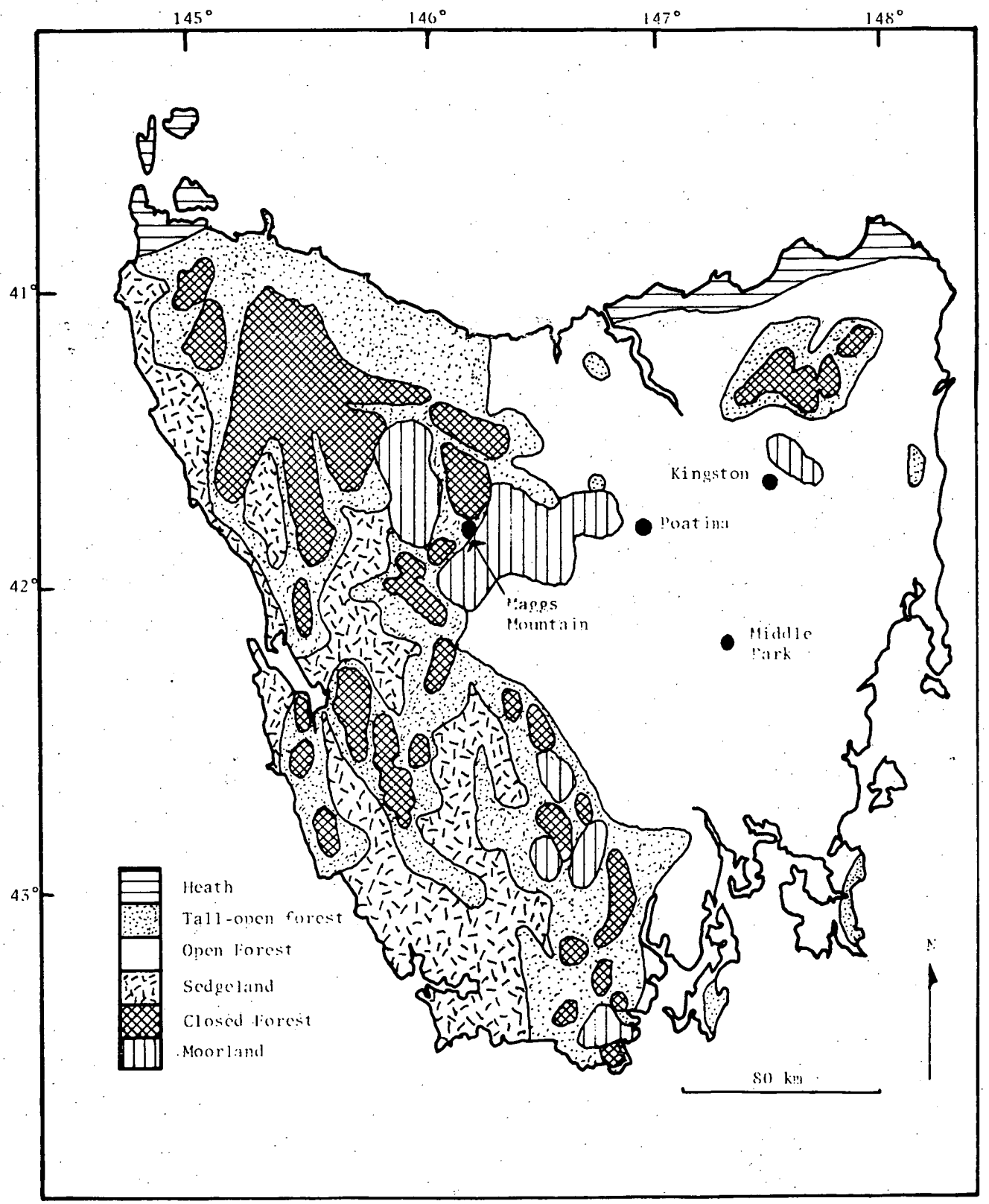
On collection the jars containing that fortnight's collection of pouch young were sealed and labelled with the date and the collection locality. The jars containing the pouch young were then catalogued into the museum collection. Unfortunately the method of collection meant that the association between the maternal skull and the pouch young was lost, resulting in data on breeding success of females being unavailable.

The skulls retained as cabinet specimens and all the pouch young collected, made up the sample examined in this study.

TABLE 3.2 Percentage of skulls retained as museum specimens from each site

Locality	Total Shot	Cabinet Specimens	% Retention
'Kingston'	327	170	52
'Middle Park'	399	114	29
Poatina	314	78	25
Maggs Mountain	76	19	25
Total	1116	381	34

FIGURE 3.1 Location of sites where populations of *T. vulpecula* were sampled during winter of 1979. The broad distribution of natural vegetation types in Tasmania is overlaid (vegetation types from a figure compiled by K. Felton, Tas. Forestry Commission).



3.3 COLLECTION AREAS

The four localities sampled are areas where Brushtail Possums are abundant and where museum staff had some personal knowledge of the area. In each locality, an experienced hunter was willing to co-operate with the museum to salvage the skulls and pouch young.

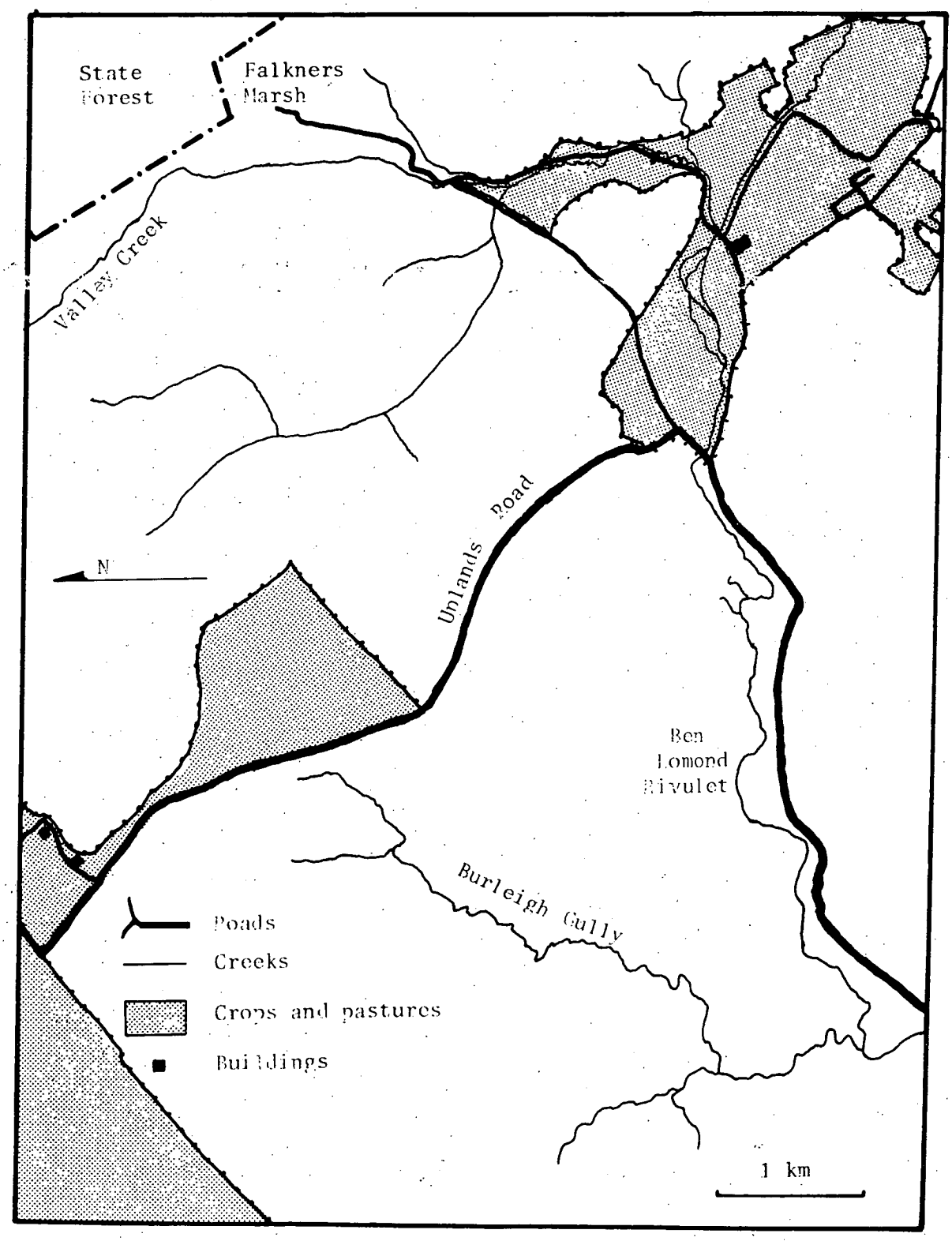
The broad distribution of natural vegetation types in Tasmania is shown in Figure 3.1. The collection localities are marked; one, Maggs Mountain, is in tall-open forest while the other three (Poatina, 'Kingston' via Nile, and 'Middle Park') are all in open forest that has been cleared and altered to differing degrees by farming. A description of the main land uses and vegetation types at each collection locality is given below.

3.3.1 'Kingston' via Nile

This is a farming property in a well watered valley on the south-west of Ben Lomond (Figure 3.2). In the valley, the arable land is sown to crops and pastures and is fertilized regularly. Remnant forest is found along the banks of creeks and rivulets. The property slopes upwards to the north and east to the foothills of Ben Lomond where it adjoins a State Forest, and to the west the hilly terrain supports open forest and woodland. In the valley floor the land is gently sloping. There are open spaces throughout the area 3 to 5 ha in extent, mostly covered with bracken, although there are some areas of pasture. Hazard reduction burning is carried out through this area. These are low intensity burns to reduce litter at irregular intervals. All the wooded area is used for rough grazing.

The vegetation is dominated by three species of eucalyptus, *Eucalyptus obliqua* (stringybark), *E. amygdalina* (black peppermint), and *E. viminalis* (white gum). Understorey plants include *Acacia dealbata* (silver wattle),

FIGURE 3.2 'Kingston' via Nile. The main forms of land use, and the general layout of roads and creeks are shown. The uncleared land supports open forest and is penetrated by numerous tracks (not shown in Figure) running off Uplands Road. Brushtail Possums were collected from all over this area shot from vehicle spotlighting along tracks. Most were taken in the thicker vegetation along the creeks, or from pasture-scrub boundaries.



Exocarpus cupressiformis (native cherry), and *Acacia botryephala* (sunshine wattle), with *Pterydium aquilinium* (bracken) and *Epacris impressa* (heath) at ground level. Lower slopes have a cover of open scrub and low stands of eucalypts (less than 27 m tall) with a crown cover of between 5 and 20%. Ascending the slopes, the stands of eucalypts become less open with crown cover up to 40% and somewhat taller, up to 35 m in height (Forest Type Series Sheet 20/5438). The species found on the property conform to the general description of the area as described by Jackson (1965) and Pinkard (1980).

The surface rock of the region is Jurassic dolerite on which stony gradational soils of a moderately permeable clay loam have developed. Rock outcrops are common on the crests and upper slopes (Pinkard 1980).

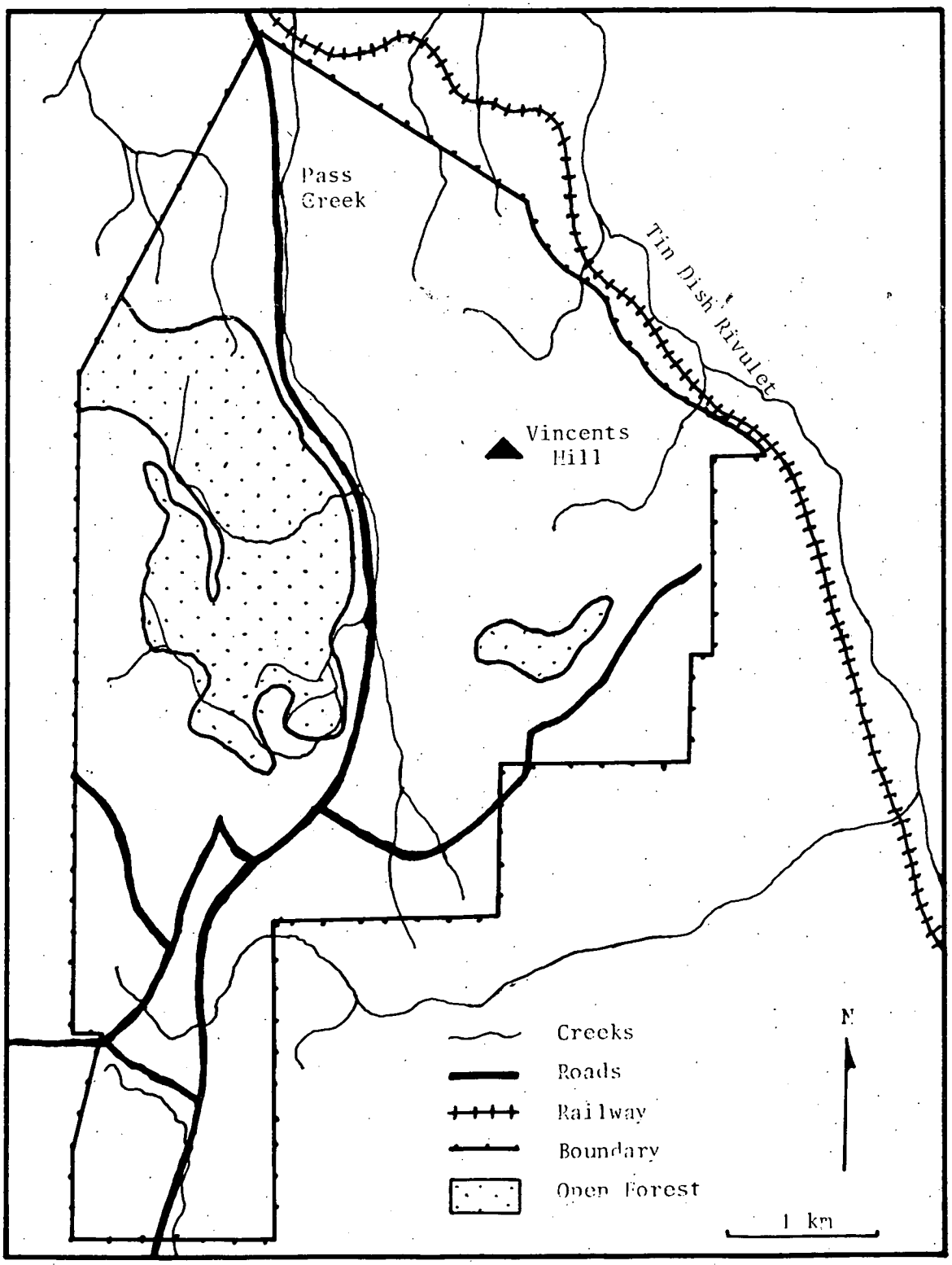
The average annual rainfall is between 750 mm and 1000 mm, distributed through the year, with a peak in the winter months. Average rainfall was received in 1979 following three years of slightly less than average falls (Tasmanian Year Book 1981).

Brushtail Possums were shot over most of the property, many being taken on pasture and cropland. A total of 327 adults were shot and 100 pouch young were collected.

3.3.2 'Middle Park'

Middle Park at Antill Ponds is a pastoral property spanning the Midlands Highway below the south-eastern slopes of the Great Western Tiers (Figure 3.3). Arable land in the valleys has been cleared and sown to pasture for many years. The pastures and the surrounding cleared hills and open woodland have been aerial top-dressed with superphosphate for the past twenty-five years. Towards the Western Tiers, the topography becomes progressively more elevated and rugged. The lightly forested hills on the property are fired whenever sufficient litter has accumulated to support a burn.

FIGURE 3.3 Middle Park showing drainage patterns and areas of woodland. The main roads on the property are shown, there are numerous tracks not shown. Brushtail Possums were shot from all over the property.



The vegetation is a woodland dominated by *Eucalyptus* species. The most important are *E. obliqua* (stringybark), *E. viminalis* (white gum), and *E. amygdalina* (black peppermint), with *E. pauciflora* (cabbage gum) present in the lower eastern part of the property. The main understorey trees are *Casurina littoralis* (bull oak) and *Acacia dealbata* (silver wattle). Poa grassland was originally present on the flat open areas which are now used for sown pasture and crops (Jackson 1965). The vegetation and species found on the property conform with those given in Jackson (1965) in a description of the typical vegetation of the area.

The surface rock of the region is Jurassic dolerite on which brown and black earths have formed (Nicolls and Dimmock 1965). The property lies in the rain shadow of the Great Western Tiers and has an average annual rainfall of 550 mm with a winter peak. In 1979, only 430 mm fell after average rainfalls in the preceding three years (Tasmanian Year Book 1981).

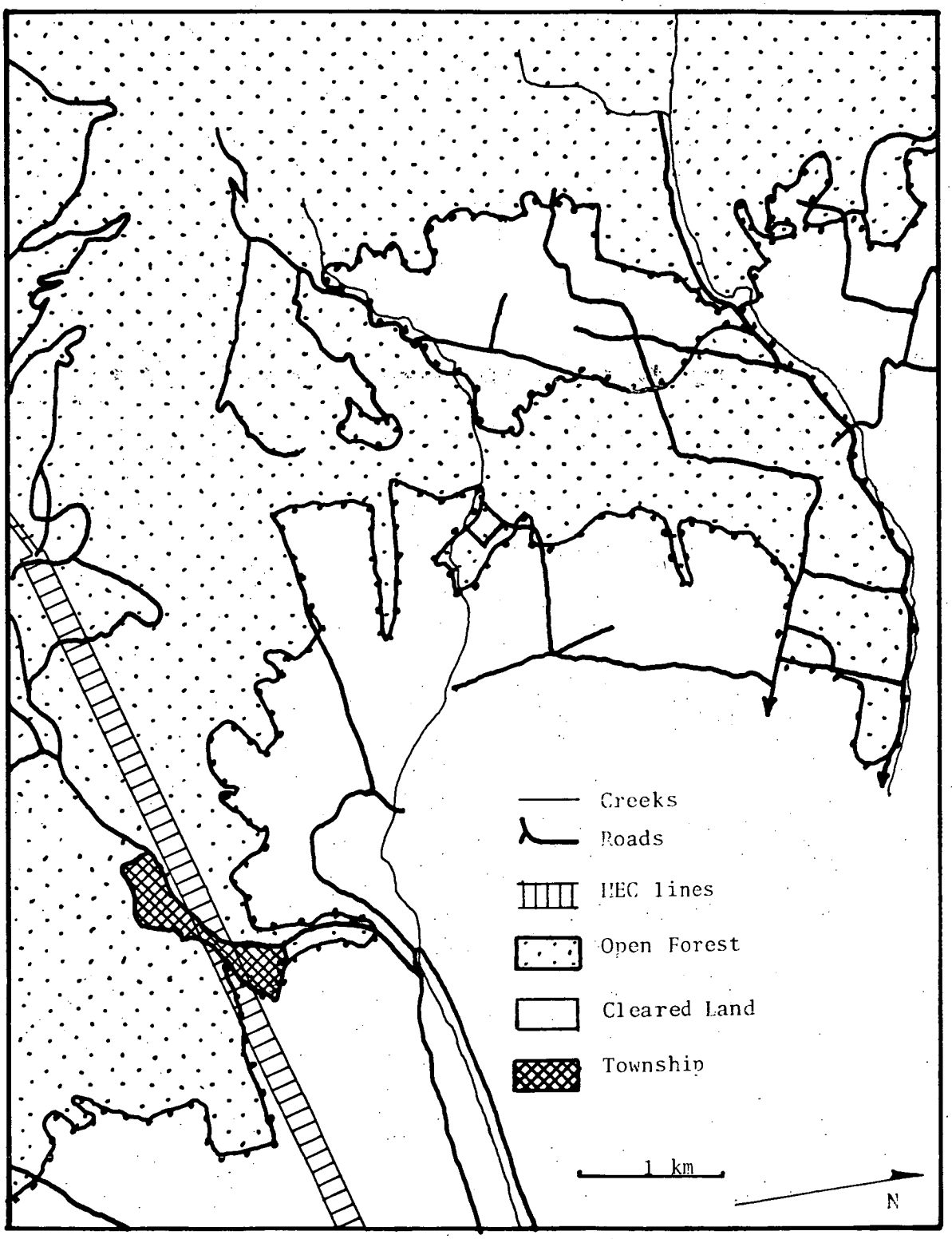
Brushtail Possums were shot over all the property. A total of 399 adults and 162 pouch young was collected.

3.3.3 Poatina

Poatina is a small village established by the Hydro-Electric Commission on the north-eastern slopes of the Great Western Tiers (Figure 3.4). Its north-eastern aspect overlooks the fertile plains of the northern midlands while, to the west and south, the Tiers rise steeply to the Central Plateau. To the north and north-east of the township, the land slopes down to flat lands which are privately owned and under cultivation. Directly west of Poatina village rise the foothills of the Central Plateau. South-west, the land rises steeply to the Plateau and is under the control of the Hydro-Electric Commission. South of the township, the land rises less steeply and is used for rough grazing.

The slopes rising to the Central Plateau from the plain of the midlands support an open eucalypt forest. The four principal eucalyptus species are *Eucalyptus delegatensis* (gum topped stringbark), *E. amygdalina* (black

FIGURE 3.4 Poatina. Brushtail Possums were collected from a vehicle spotlighting along roads in and near the forest boundary.



peppermint, *E. viminalis* (white gum), and *E. obliqua* (stringybark). *E. delegatensis* tends to predominate on the upper slopes, the other species lower down. Where present, the understorey is mainly wattle species, *Acacia melanoxylon* (blackwood) and *A. dealbata* (silver wattle). Bracken fern is present in lower areas. South of the township, the vegetation consists of mature stands of eucalypts with a crown cover of between 20 and 40%, and is used for rough grazing (Forest Type Series 20/4937 1971). West of the township the lower slopes are covered with scrub and bracken with isolated stands of eucalypts with a crown cover of less than 50%. Further up the slopes are stands of mature eucalypts (up to 40 m in height) with crown cover around 70% (Forest Type Series 20/4937 1971). This area is also used for rough grazing.

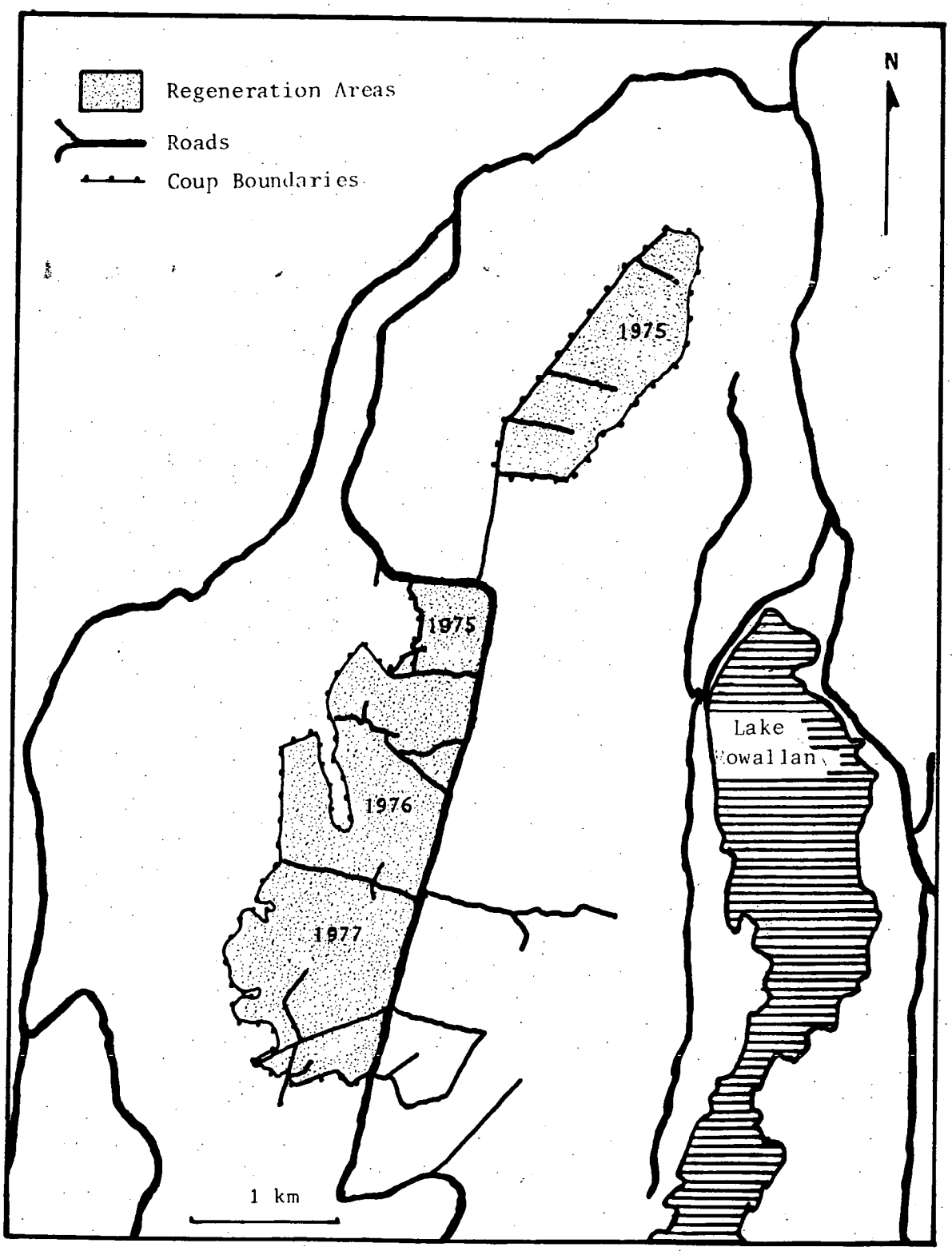
Poatina itself is at an altitude of 400 m; the Central Plateau to the west of the township is at an altitude of 1200 m (Lands Department Topographic Survey 1975). The average rainfall in the area is around 1000 mm per annum with a winter peak. Average rainfall was received in 1979, which was also the case in the preceding three years (Tasmanian Year Book 1981).

Brushtail Possums were taken from the forested slopes around and above Poatina, most being shot in the forest margins and areas used for rough grazing. A total of 314 adults with 108 pouch young was collected from the locality.

3.3.4 Maggs Mountain

Maggs Mountain is an elevated plateau, 880 m above sea level, between the Mersey and the Arm Valleys to the west of Lake Rowallan (Figure 3.5). The plateau has been subjected to progressive clearfelling of forest compartments for timber (Green 1977). These compartments are between 30 ha and 50 ha in extent and have been sown with *Eucalyptus delegatensis* (gum

FIGURE 3.5 Regrowth compartments of *E. delegatensis* on Maggs Mountain. Dates of regeneration planting are shown in each compartment. Brushtail Possums were spotlighted and shot from the forestry trails in the area, being taken from regrowth and adjoining forest.



topped stringybark) after regeneration burns between 1975 and 1978. This regrowth was one to three years old at the time the sample was collected.

The dominant tree species in the area is *E. delegatensis*, there being an open forest of this species surrounding the regeneration areas. Trees in this forest are up to 40 m in height and with a crown cover of between 20 and 70% (Forest Type Series 20/4338). There is an understorey of rain-forest species, predominantly myrtle (*Nothofagus cunninghamii*) less than 24 m tall with sassafras (*Artherosperma moschatum*) as a minor species (Richley 1978).

The average rainfall is 1600 mm. In 1979 average rainfall was received following three previous years of average rainfall.

The Tasmanian Forestry Commission has had a problem with browsing damage to eucalyptus regeneration in the area and, during the winter of 1979, an investigation to identify the culprit species and test the effectiveness of 1080 poisoning was carried out on Maggs Mountain. Brushtail Possums were shot from a vehicle spotlighting along the logging roads in the regeneration areas and surrounding forest. A total of 76 adults with 27 pouch young was taken from this area.

3.4 DERIVATION OF AGE CLASSES

3.4.1 Adults

Tooth wear has long been used as an indicator of age in mammals. Kean (1975) and Winter (1980) gave methods which could be used successfully in field and laboratory situations with Brushtail Possums. The method given by both authors described seven classes of tooth wear based upon the pattern of pulp and dentine exposed in the molariform teeth.

The patterns of wear on the first upper molar as described by Winter (1980) were used to assign age classes to the skulls. The patterns of wear are shown below (Figure 3.6).

FIGURE 3.6 Classes of tooth wear of the top left first molar of *T. vulpecula* (from Winter 1980). Exposed dentine is black. Anterior at top, lingual at left.

Wear Class	Crown of M^1	Description
1		Cusps high and pointed with no apparent wear
2		Lingual cusps with points rounded but with no dentine exposed
3		Small crescents of dentine exposed on lingual cusps, but none on labial cusps
4		Crescents of dentine on lingual cusps larger, but cusps still high and rounded; dentine exposed on at least one labial cusp, but not joined to dentine crescents of lingual cusp
5		Lower limit: dentine of at least one labial cusp joined to dentine crescent of lingual cusp
		Upper limit: dentine of lingual cusps joined, no longer appearing as crescents; dentine of both labial cusps joined to lingual cusps, but still appear as narrow strips along the cusp ridge
6		Lower limit: lingual cusps flattened, and broad band of exposed dentine between the two; dentine on labial cusps no longer a narrow strip but a broad band
		Upper limit: both lingual and labial cusps flattened, with large areas of exposed dentine, but still with an enamel indentation between anterior and posterior lingual cusps
7		Cusps completely obliterated and crown of tooth dished; no enamel indentation between anterior and posterior lingual cusps.

The relationship between the molar wear class and the age in years of known-age Brushtail Possums is shown in Table 3.3.

TABLE 3.3 Age ranges corresponding to molar wear class, data from Winter (1980).

Molar Wear Class	Age Range in Years
1	<2
2	>1-<3
3	>2-<5
4	>3-<5
5	>4-<8
6	>5
7	>6

The relationship between tooth wear and age is subject to two major sources of error, one being variation in the rate of wear of individual teeth both within and between populations, and the other being observer error.

Variation in the rate of tooth wear is considered to be largely due to variations in the character of the diet (Hocking 1981). The major food source in all areas was eucalyptus species, and so the rate of tooth wear was assumed to be relatively constant both within and between areas.

Observer error was minimised by having one observer take all readings; later blind checking found no discrepancies. Winter (1980) described difficulties in taking measurements as he was working with live animals so that the awkward angle of observation and the wet glistening surface of the tooth caused problems with accurate classification. These problems were obviously not found in the present study.

The molar wear class can be used to assign an age range in years to the possum. Improved correlation between wear patterns and age could be obtained by checking against a technique such as cementum deposition described by Pekelharing (1970). This method, although providing a more

precise measure of the age in years, was not used in the present study as it would have necessitated the destruction of museum specimens, the facilities to do so were not available and it is both time consuming and laborious. Molar tooth wear classes were used to provide a ready estimate of the age structure of the population.

All the skulls available for examination from the four populations were classified on the basis of molar tooth wear (Table 3.4).

TABLE 3.4 Numbers of animals in each molar wear class from each locality.

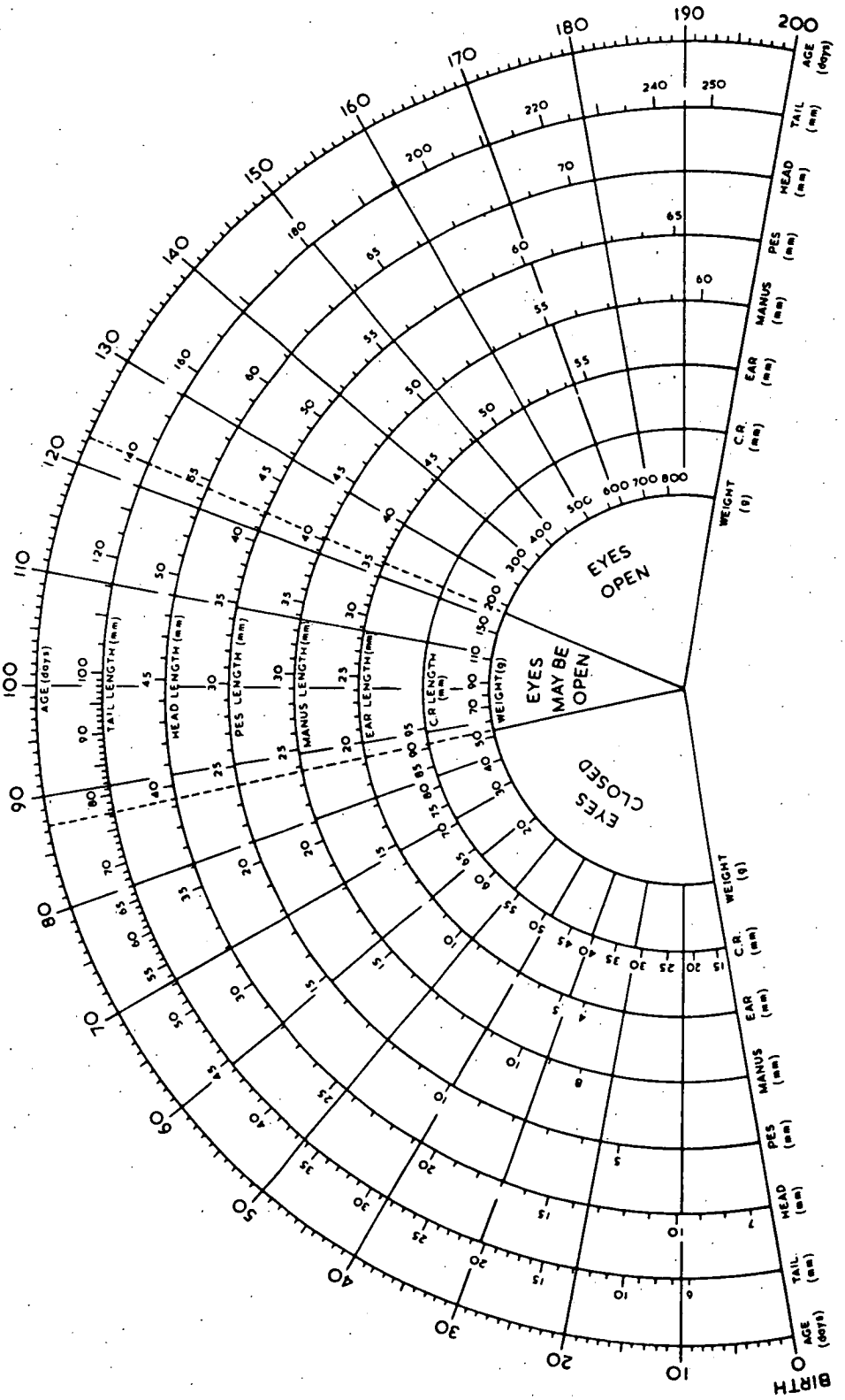
Molar Wear Class		1	2	3	4	5	6	7
'Kingston'	Male	9	21	29	19	13	9	3
	Female	5	16	15	12	12	4	3
	Total	14	37	44	31	25	13	6
'Middle Park'	Male	3	23	25	10	3	4	1
	Female	1	8	18	8	8	1	1
	Total	4	31	43	18	11	5	2
Poatina	Male	1	7	7	6	6	7	2
	Female	5	7	9	6	10	2	3
	Total	6	14	16	12	16	9	5
Maggs Mountain	Male	0	2	3	2	2	0	0
	Female	0	3	3	1	2	0	1
	Total	0	5	6	3	4	0	1
All Localities	Male	13	53	64	37	24	20	6
	Female	11	34	45	27	32	7	8
	Total	24	87	109	64	56	27	14

3.4.2 Pouch Young

An age in days was assigned to each pouch young using the nomogram* of Lyne and Verhagen (1957) (Figure 3.8). A copy of the nomogram was fixed to cardboard and a cotton thread passed through the origin. The free end of the thread was moved across the board to give a direct reading of the age in days for each measurement taken. Each pouch young was sexed and a series of measurements taken, the particular set chosen depending upon the size of the pouch young. On very small animals, the only measurements taken were the crown-rump and head length. For larger pouch young

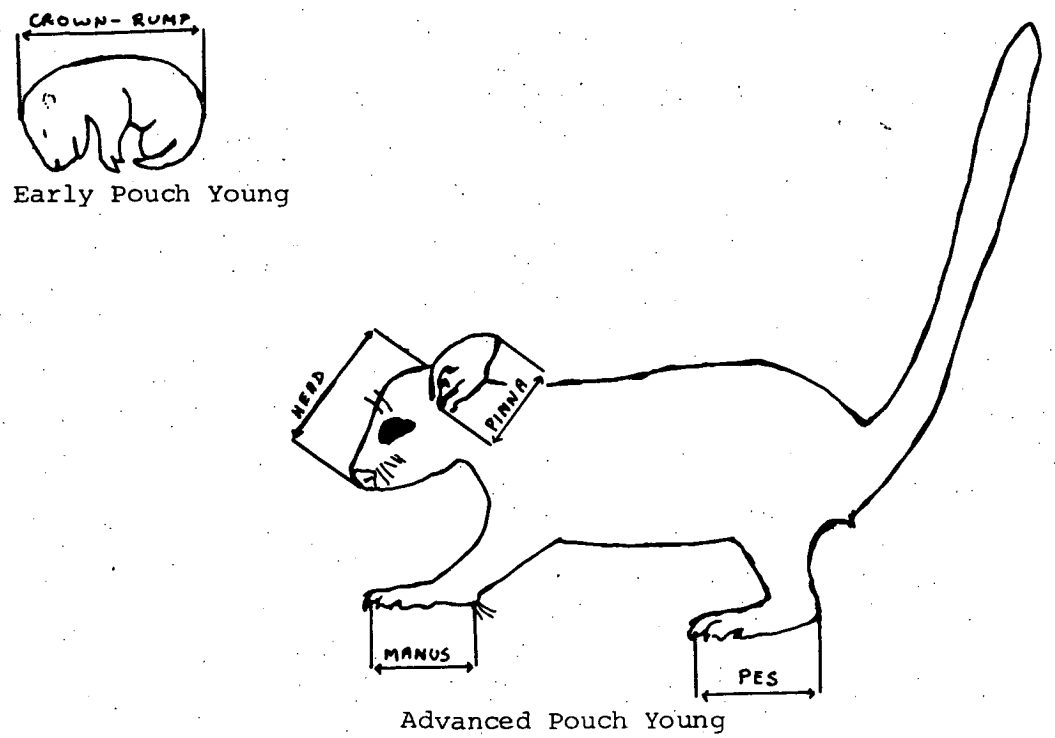
* The decision to use the nomogram in preference to regression analyses is discussed in Chapter 6.

FIGURE 3.7 *Trichosurus vulpecula*. Nomogram for determining the age in days of pouch young (from Lyne and Verhagen 1957).



the measurements included head, manus, pes and pinna (Figure 3.8). Tail length was not used as previous experience with Sydney populations of the Brushtail Possum had shown it to be unreliable (James, personal observation). Measurements to the nearest millimetre were taken using vernier calipers.

FIGURE 3.8 Pouch young of *T. vulpecula* identifying measurements taken for age determination (after Lyne and Verhagen 1957).



The various parameters measured, in general, gave a very narrow range of ages in days. The age of the pouch young in days was taken as the mean of the ages indicated by each measurement. From the estimated age of the pouch young at death the probable date of birth was calculated. The estimated day of birth for each pouch young at each locality is included as Appendix A. The overall distribution of births in all populations is shown (Table 3.5) to provide a readable summary of this information.

TABLE 3.5 Distribution of births per/week at each site

Month	Week No.	Kingston	Middle Park	Poatina	Maggs Mt.	Pooled
	3		1			1
JAN	4					
	5					
	6		2			2
FEB	7					
	8					
	9					
	10					
MAR	11	1	3			4
	12	3	4			7
	13	3	8	2		13
	14	4	25	2		31
APR	15	22	16	13		51
	16	18	26	16	1	61
	17	15	26	17	2	60
	18	11	18	17	6	52
MAY	19	4	10	16	5	35
	20	4	6	9	4	23
	21	3	7	5	3	18
	22	3	3	2	1	9
	23		2	4	3	9
JUNE	24	4	2	2		8
	25		1	1	1	3
	26	1		1		2
	27	2	1			3
JULY	28	1		1	1	3
	29		1			1
	30	1				1
	31					
	32					
AUG	33					
	34	— Latest sampling during 1979				
	35					
Total Births		100	162	108	27	397

3.5 SUMMARY

Skulls and pouch young from four separate populations of Brushtail Possums were salvaged by the Queen Victoria Museum, Launceston. This material was collected with the co-operation of commercial hunters and catalogued and cleaned by museum staff. It is now kept at the museum.

The hunting took place in areas where Brushtail Possums were locally abundant and large numbers were collected. It is assumed that the samples collected are representative of the parent populations.

The pattern of wear on the first upper left molar M^1 was used to divide the samples into wear classes as described by Winter (1980). The molar wear classes gave a ready estimate of the age structure of each population. The age at death of pouch young was estimated using the nomogram of Lyne and Verhagen (1957). This data is later used to describe the age structure and breeding patterns found in each of the four populations.

CHAPTER 4 BREEDING PATTERNS AND PRODUCTION OF YOUNG

4.1 INTRODUCTION

The frequency of breeding and the size of resulting litters in any mammalian species are adaptive features that have evolved in response to a range of factors. Under the influence of these factors a breeding pattern develops that is geared to maximise the ability of the species to exploit the ecological niche it occupies.

A measure of the number of young produced by a population is an estimate of the capacity of the population to produce individuals available for recruitment into the parent population. The rate of production of young by a population determines, in part, its potential for increase. It is critical in determining the capacity of the population to recover from a reduction in numbers as a result, for example, of hunting, pest control programmes or environmental disturbance.

Breeding patterns displayed in each of the four populations of *T. vulpecula* are examined here. The likely production of independent juveniles by each population is assessed. Factors known to influence the production of young in possums are discussed in terms of their effects on the populations examined in this study.

Reproductive and behavioural patterns of populations of *T. vulpecula* vary according to the habitat occupied over the range of the species. Minor variations across a number of parameters affecting breeding success can add up to a large effect on the reproductive rates of populations of

T. vulpecula (Crawley 1973). Breeding patterns found in the four populations examined are compared to those of other populations.

4.2 BREEDING PARAMETERS

The rate of production of independent young by populations of *T. vulpecula* is affected by a number of breeding parameters. These have been given as the number of breeding seasons per annum, the age at which reproductive maturity is achieved, and the breeding success of mature females, i.e. the survival of pouch young to independence (Crawley 1973). Variation in litter size is not a factor affecting the rate of production of pouch young in *T. vulpecula* as multiple births are a rare phenomenon in wild populations.

T. vulpecula is a seasonal breeder with the main period of births occurring in autumn. Female possums have been recorded as first giving birth at all ages between one and four years in various populations. Most mature females have been found to give birth at least once each year. The rate of survival of pouch young to independence is generally high, but shows some variation between populations.

As noted by Brockie *et al.* (1979) these parameters of breeding success are correlated with each other, but the factors that affect reproductive variation are obscure. However, it appears that fluctuations in local environments play a more important role than either latitude or daylength.

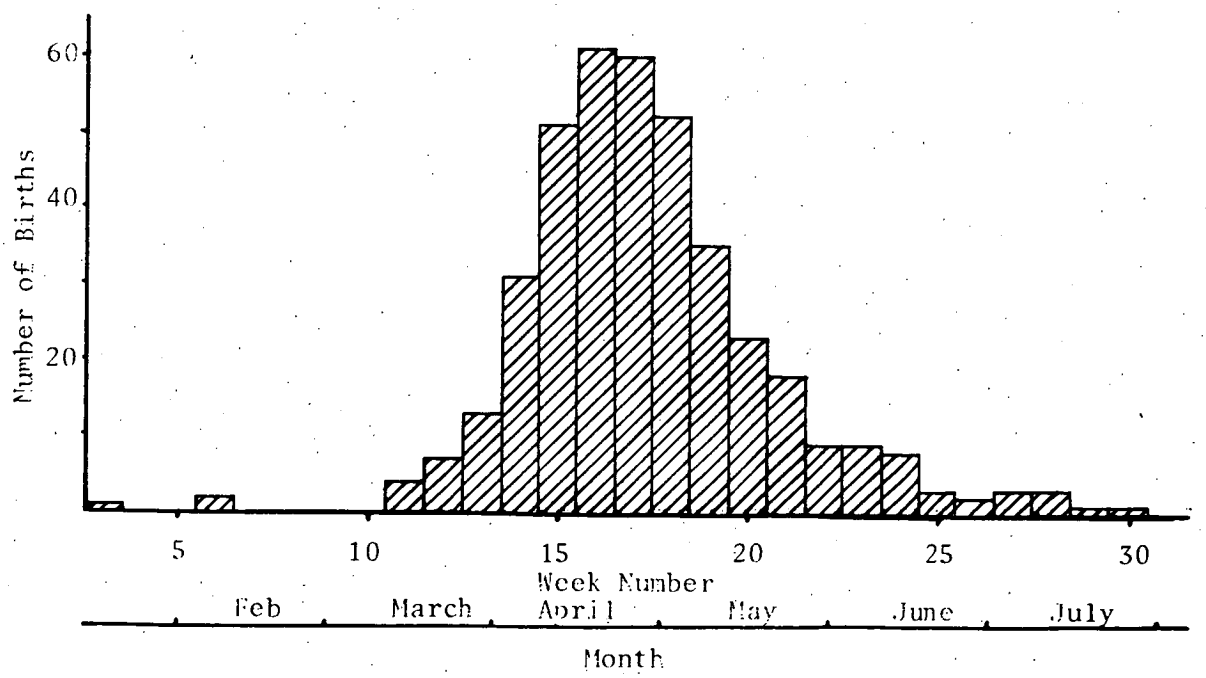
4.2.1 Breeding Season

The pattern of breeding was examined using data on birth dates extrapolated back from estimated ages of pouch young. Birth dates calculated in this manner are subject to an error which increases with the time since birth. Hocking (1981) studied comparative rates of growth of pouch young in several populations in southern Tasmania and found no deviation in the

growth rates of pouch young from the nomogram of Lyne and Verhagen (1957) for animals less than 120 days of age. This is assumed to be so for the populations examined in this study as well and, as less than 7% of the pouch young sampled had estimated ages in excess of 120 days, this source of error was regarded as insignificant. In any case, this error would not affect the estimates of mean dates of birth but would affect estimates of variance about the mean. Similarly the error of up to seven days in the known date of death would affect estimates of variance about the mean.

A total of 397 pouch young from all four populations was examined and assessed for age. The distribution of births, after pooling the data from all localities, is shown (Figure 4.1).

FIGURE 4.1 *Trichosurus vulpecula*. Seasonal distribution of 397 births in Tasmania during 1979. Class interval 7 days. Median date of birth 25 April.



During the autumn, births start in March, rising to a peak during April and tapering off during June and July. The mean date of all births was the 23 April, the median date the 25 April.

In pooling the data, any variation in the breeding season in different areas was obscured. Therefore, the pooled data has been partitional according to locality. An examination of Figure 4.2 suggests that each locality differs in the onset of the main breeding period.

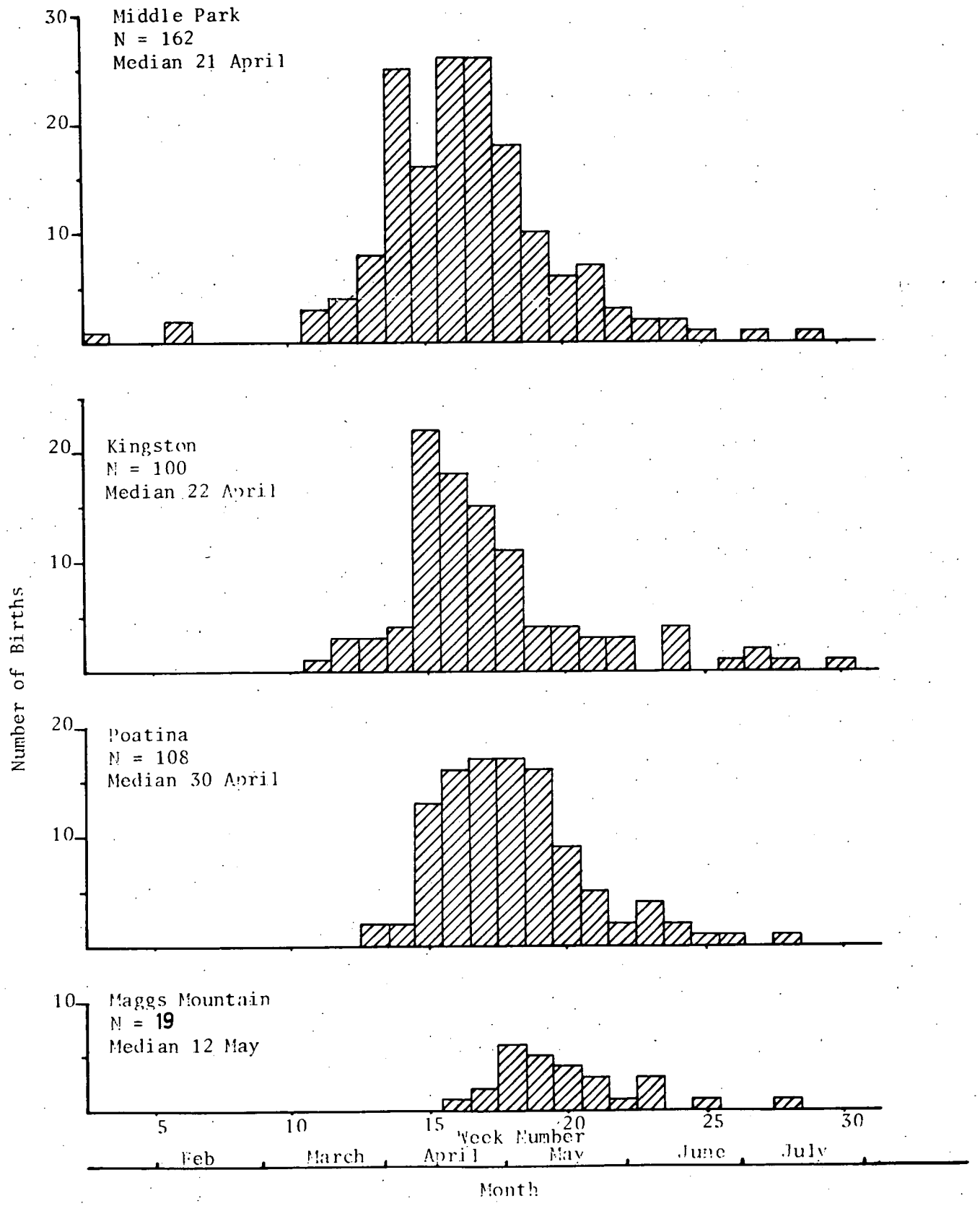
The range of estimated dates of birth provided an index of the duration of the breeding period at each locality. Testing with Chi-square showed significant differences at the 1% level in the duration of the breeding season. This implies that the duration of the breeding season varied between localities. The breeding season ended at approximately the same time (see Figure 4.2) for each population, so those populations with an earlier onset of the breeding season would appear to have a more extended breeding period (Table 4.2).

TABLE 4.2 Length of the breeding season at each locality.

Locality	Median Date of Birth	95% of Births Between -	Length of Main Breeding Season (Days)
Middle Park	21 April	14 March-17 June	95
Kingston	22 April	14 March-12 June	90
Poatina	30 April	13 April-22 June	70
Maggs Mt.	14 May	23 April-17 June	55

Three births were detected outside the main breeding season. Two were estimated to have occurred in February and one in January. All were from the Middle Park population where the duration of the breeding season was longest and which had the earliest median date of birth.

FIGURE 4.2 Distribution of all births at each of the four localities during autumn and winter of 1979. Class intervals are seven days. The median date of birth is given together with the sample size (N). The last sample at each locality was taken on about 26 August (week 34).



That there was considerable variation in the timing of breeding for females from the same habitat is evidenced by the length of the breeding season. Hocking (1981) suggested that a failure to conceive at first oestrus could cause an extension of the breeding season as birth would occur during the next oestrous cycle (that is, three to four weeks later); hence, much of the variation within a population could be due to a failure to conceive at first oestrus.

It appears unlikely that this is the most important factor controlling the duration of the breeding season in these populations. The duration of the breeding season appears to be closely related to the habitat type and local conditions each population experiences. Thus, females in populations where there is a lengthy breeding season have more opportunity to compensate for a failure to conceive, or for the loss of an early pouch young, than do females in populations with a more restricted breeding season.

It appears that, where that habitat is a dry open woodland, the populations of Brushtail Possums breed early and long; as the habitat quality becomes less optimal for possums, the peak of the breeding season is later in the autumn and the season is more restricted. The relationship between habitat type and parameters of breeding success is discussed more fully later in this chapter.

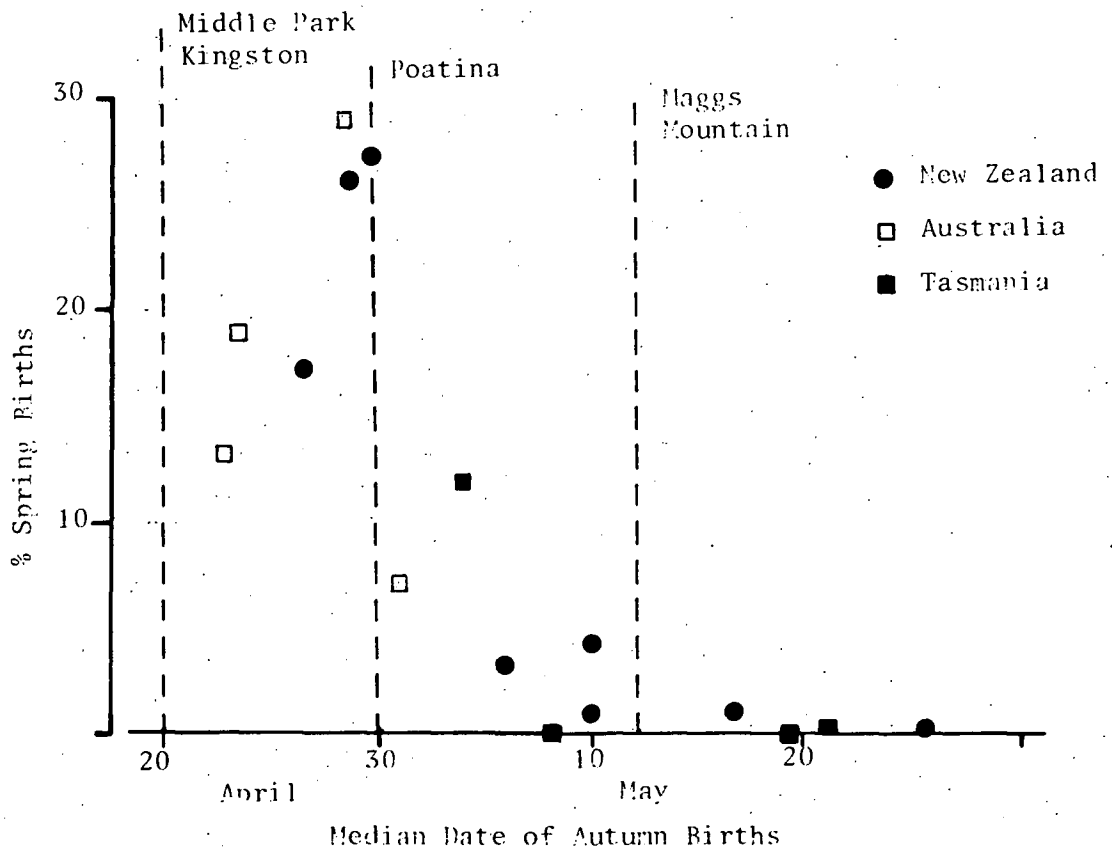
As sampling of these populations was carried out during the winter months (June, July, and August), it was not possible even by extrapolation of known lactation periods to detect births which occurred the previous spring. The contribution made by spring births to the reproductive output of these populations is therefore unknown.

There are no substantiated records for high levels of spring breeding in Tasmanian populations, although spring births have been recorded at various localities. Hocking (1981) found no evidence of spring births in

populations living in the tall open forests of southern Tasmania except for one population in 4-5 year old regrowth where the median date of birth was 1 May. On Flinders Island, in open forest and heath, there appears to be a main autumn breeding season with occasional births in spring (R. Rose, personal communication). Some spring births have been found in populations living in similar habitat on the Tasmanian mainland (R. Rose, personal communication).

Brockie *et al.* (1979) demonstrated that there is a correlation between the proportion of spring births and the timing of the main autumn breeding season (Figure 4.3).

FIGURE 4.3 Relationship between the median date of autumn births and the percentage of spring births in Australian and New Zealand populations of *T. vulpecula* (from Brockie *et al.* 1979).



If the relationship between median date of autumn births and the proportion of spring births holds good for these populations, then the *T. vulpecula* populations at Kingston and Middle Park would be expected to show.more than 15% spring births, Poatina population more than 5%, and the Maggs Mountain population nil. The Maggs Mountain site is 1-3 year old regrowth of tall open forest, similar to some of Hocking's study sites, where he found no evidence of spring breeding and approximately the same median date of birth. The drier, more open habitats support populations with earlier median dates of birth, earlier than previously recorded in Tasmania where the median dates of birth have been in May (Lyne and Verhagen 1957; Hocking 1981). They approximate the median dates of birth for populations living in eucalyptus woodlands on the Australian mainland (Lyne and Verhagen 1957; Dunnet 1964; Smith *et al.* 1969).

4.2.2 Incidence of Breeding

There are several estimates used to measure the incidence of breeding in a population. Fecundity is a measure of the ability to conceive, and is defined as the ratio of *in utero* young to the total number of adult females (Giles 1978). Fecundity is estimated in this study, as it has been in other studies of this species, as the ratio of pouch young produced to the total number of adult females (Table 4.3). The net natality is the number of female offspring produced (Giles 1978). It therefore, gives a maximum value for the potential of the population to increase under a given set of environmental conditions. It is measured as the ratio of female young produced to the total number of adult females in the population (Table 4.4).

There are two obvious sources of error in the estimates of fecundity and net natality for these populations. In the first place, the time of sample collection meant that the period of spring breeding, if present, was not sampled. Therefore the number of young produced per annum will be

an underestimate for populations where there are spring births. Secondly, the age at reproductive maturity for females in these populations is unknown. Females less than 2 years old are excluded from the calculations so that all females two years and over are considered to be reproductively mature. This is the age at which female *T. vulpecula* generally reach maturity and start breeding (Smith *et al.* 1969; Hocking 1981), although the onset ot first breeding may be at 12 months (How 1981) in some populations, or delayed to three or four years in others (Crawley 1973).

Altogether, 516 female skulls were collected along with 397 pouch young. The method of collection and storage meant that the association between a female and her offspring was lost, so no estimates of the level of breeding by females at different ages could be made. The allocation of adults to year classes on the patterns of molar tooth wear is described in Chapter 5.

TABLE 4.3 Estimates of the fecundity of female *T. vulpecula* from populations at four localities.

Locality	Total Females	Female 2 years and Older	Pouch Young	Fecundity (%)
Kingston	130	113.9	100	87.8
Middle Park	184	173.0	162	93.6
Poatina	154	131.6	108	82.0
Maggs Mt.	36	33.5	27	80.5

Previous studies have shown that, among females two years and older, the breeding rate is generally high - more than 80% of females giving birth each autumn in most populations in Australia and New Zealand (Brockie *et al.* 1979). These populations show the same high level of autumn breeding generally found in other populations of *T. vulpecula* across the range of the species.

TABLE 4.4 Estimates of the net natality of female *T. vulpecula* from populations at four localities.

Locality	Total Females	Females 2 Years and Older	Female Pouch Young	Net Natality (%)
Kingston	130	113.9	50	43.9
Middle Park	184	173.0	68	39.3
Poatina	154	131.6	62	47.1
Maggs Mt.	36	33.5	8	23.9

The net natality is a measure of the number of female offspring produced by a population and, as such, is a measure of that population's maximum potential for increase under a given set of conditions. The Poatina population has the highest net natality and thus the greatest potential for increase of the four populations examined. The fecundity of this population is not particularly high but an excess of female births raises the estimate of the net natality. Similarly a large excess of male births in the Maggs Mountain population lowers the estimate of the net natality.

4.2.3 Sex Ratios of Pouch Young

The sex ratio for all pouch young collected at each locality is given in Table 4.5.

TABLE 4.5 Proportion of male pouch young in each population

Locality	Pouch Young	Proportion of Males	χ^2
Kingston	100	0.50	0.00
Middle Park	162	0.58	4.17*
Poatina	108	0.44	1.33
Maggs Mt.	27	0.74	7.26**

* Significant at 5% level; ** significant at 1% level

The bias in favour of male pouch young in the Maggs Mountain and Middle Park populations accounts for much of the observed variation in the estimates of net natality.

Hocking (1981) examined sex ratios of pouch young in different-aged eucalypt regeneration areas. He found that the sex ratio did not differ significantly from unity except in areas 0-4 years after a regeneration burn. This is similar to the Maggs Mountain habitat and a similar highly significant bias in favour of male pouch young was found.

Sex ratios biased towards male pouch young have been found in other studies of *T. vulpecula*. Hope (1972) combined the data on pouch young from a number of studies, including his own, to examine the sex ratio of pouch young. He found a consistent and significant excess of males. Table 4.6 shows Hope's results; included also are the pouch young from Hocking's (1981) study and from this study.

TABLE 4.6 Sex of *T. vulpecula* pouch young from different surveys

Reference	Number of Young			χ^2
	Male	Female	Total	
Tyndale-Biscoe 1955	69	59	128	0.78
Dunnet 1956	11	6	17	1.47
Lyne & Verhagen 1957	71	66	137	0.91
Caughley & Kean 1964	332	294	626	2.31
Smith *et al.* 1969	81	74	155	0.32
Hope 1972	113	94	207	1.74
Hocking 1981	94	68	162	4.17
This study 1984	212	185	397	1.84
Total	983	846	1829	5.13*

* $0.01<P<0.05$

Thus, there appears to be a consistent trend towards an excess of male births in *T. vulpecula* populations in a variety of habitats. In aggregate, the distribution of sex in pouch young is 54% male, 46% female. This trend is not followed in the Poatina population where the distribution of sex in pouch young is 44% male, 56% female.

4.2.4 Duration of Pouch Life

An estimate of the duration of pouch life in each population was made by examining the numbers of the oldest pouch young taken in each area. Advanced pouch young made up about 7% of the sample giving 27 pouch young for examination. The age distribution of these young is given in Table 4.7.

The 95% limits of the breeding season at each locality (Table 4.2) were used to calculate the maximum possible age that could be detected for a young born during the main autumn breeding season given that the last sample was taken from each population on or just before 26 August, 1979.

Pouch young approaching or exceeding the maximum detectable age were collected from all localities indicating that pouch life was longer than this period.

The capture/release study of Hocking (1981) found no young less than 170 days taken other than in the mother's pouch, and the oldest animal taken within the pouch was 198 days. Young have previously been recorded as first leaving the pouch at 121 days (Dunnet 1956), with the oldest young taken within the pouch at 170 days (Dunnet 1956; Smith *et al.* 1969).

The limited information on the duration of pouch life (Table 4.7) suggests that the extended period of pouch life found by Hocking (1981) for *T. vulpecula* in southern Tasmania is the norm for the populations examined in this study as well.

TABLE 4.7 Estimated age in days of pouch young more than 120 days old at the time of collection.

Locality	Age	Date of Birth	Maximum Detectable Age
Middle Park	170	20-1-79	165 days
	178	9-2-79	
	134	11-2-79	
	160	13-3-79	
	148	25-3-79	
	130	28-3-79	
	143	31-3-79	
	125	3-4-79	
	135	7-4-79	
	125	17-4-79	
	125	17-4-79	
Kingston	160	13-3-79	165 days
	122	6-4-79	
	124	18-4-79	
	124	18-4-79	
	121	21-4-79	
Poatina	131	28-3-79	135 days
	139	3-4-79	
	132	10-4-79	
	127	15-4-79	
	127	15-4-79	
	126	16-4-79	
	125	17-4-79	
	120	20-4-79	
	122	20-4-79	
	120	20-4-79	
Maggs Mountain	123	20-4-79	125 days

4.3 CORRELATIONS BETWEEN BREEDING PARAMETERS

The breeding parameters presented here will be discussed in comparison with similar parameters in other populations of *T. vulpecula*. This is done, firstly, in order to relate the production of young in these populations to variations found within the species and, secondly, to relate this variation in breeding to differences in habitat.

The seasonal distribution of births is consistent with the findings of previous studies of *T. vulpecula*. Births occurred during a restricted period from late March to the end of June with the median date for all births the 25 April. This date coincides with those recorded for mainland Australian populations where the median date of birth also falls in April (How 1972; Dunnet 1956; Smith *et al.* 1969). It is around three weeks earlier than the median date of birth found for populations of *T. vulpecula* inhabiting tall-open forest in southern Tasmania (Hocking 1981), where the median date of birth coincided with the later dates recorded for New Zealand populations (Clout 1977; Bamford 1973; Bell 1977).

The figure given for the median date of all births is a composite of four separate samples and the variation in median dates of birth between the samples is considerable. The reported range of median dates of birth for Tasmanian populations is from 21 April for a population in dry open woodland (this study) to 1 June for a population inhabiting 30-40 year-old regrowth of tall-open forest (Hocking 1981). This covers the range of median dates of birth recorded for *T. vulpecula* across the geographic distribution of the species.

The occurrence of a spring breeding season has been noted in a number of populations where it may contribute up to 30% of the total births (Dunnet 1964; Clout 1977). It is almost totally absent from other populations (Crawley 1973; Hocking 1981). A correlation between median date of births

in autumn and the level of spring births has been noted by Brockie *et al.* (see Figure 4.3). The early median dates of birth found in the populations from woodland (Kingston and Middle Park) implies that there may be a high percentage of spring births in these populations.

It follows from the earlier assumption (Section 4.2.4) that pouch life is at least 170 days in these populations and, given that weaning occurs no less than 40 days after first emergence from the pouch that females from these populations would return to oestrus around 210 days after the birth of a pouch young in autumn that was reared to independence. Adding this period to the median dates of birth given earlier shows the peak of spring births, if they occur would be around mid November for the Kingston and Middle Park populations, somewhat later (4-6 weeks) than the main period for spring births found in mainland populations (Dunnet 1956; Smith *et al.* 1969).

Hope (1972), combining data from all available sources, was able to show, as has the present study, a bias towards male pouch young. Sex ratios favouring males at birth have been found in many eutherian mammals (Crew 1952). However, among marsupials studied, only the Grey Kangaroo (*Macropus giganteus*) has been reported to have a higher proportion of males at birth (Caughley and Kean 1964) although subsequent samples of this species have failed to detect this bias (Poole 1975). The bias in favour of male births for *T. vulpecula* was not consistent for all samples and, for one population (Poatina), female births exceeded male births. The one highly significant result ($P<0.01$ in favour of male pouch young) was from a population in 1-4 year old eucalypt regrowth from a tall-open forest. It is noteworthy that Hocking (1981), examining the sex ratio of pouch young from populations inhabiting various stages of regrowth of tall-open forest, found the same highly significant bias towards male pouch young for populations from the same age regrowth. He found no significant bias towards male pouch young from populations inhabiting older stages of regrowth.

Most studies of *T. vulpecula* indicate a survival rate amongst dependent pouch young in excess of 90% (Tyndale-Biscoe 1955; Dunnet 1964; How 1972; Clout 1977). In the review of breeding patterns in *T. vulpecula* by Brockie *et al.* (1979), a significant correlation ($P<0.02$) between the median date of autumn birth and the survival of pouch young was noted. As survival of pouch young could not be estimated directly for the populations studied here, it is assumed that this relationship is true for these populations. Hence survival of pouch young in the Middle Park, Kingston, and Poatina populations is expected to be in excess of 90%; survival in the Maggs Mountain population is expected to be somewhat lower at around 75%. However, Hocking (1981) found that the rate of survival for pouch young from a population in habitat similar to Maggs Mountain in southern Tasmania was close to 100%. The assessment of the survival rate of pouch young given here is the minimum expected from the relationship between median date of birth and survival rate described by Brockie *et al.* (1979), and may well exceed this.

4.4 YOUNG AVAILABLE FOR RECRUITMENT

The estimate of net natality made earlier gives a measure of the capacity of a population to expand in a given environment. It is essentially the number of female offspring per adult female per year. Brushtail Possums do not start breeding until they reach an age of at least 12 months and more generally 24 months (Smith *et al.* 1969).

All females estimated to have reached an age of two years or more were included in the calculation of the net natality. Females less than two years of age were not included for several reasons:

(1) not likely to be reproductively mature;

(2) if carrying young, unlikely to raise it to independence (How 1981);

(3) under represented in sample because of more cryptic behaviour patterns and shooter bias against small animals;

(4) probably transients and not yet members of the resident adult population.

The two year and over group of females are thus thought to be responsible for all effective production of young. It is possible that not all females of this age in each population are reproductively mature, hence the net natality has been calculated for all probably mature females rather than all that actually are mature.

The effective birth rate is the number of female young raised to independence. It is estimated as the number of female young raised to independence per female per annum. Assuming the average age at reproductive maturity is 24 months in each population, the effective birth rate for each of the four populations has been calculated. The survival rate of pouch young is estimated to be the minimum expected from the correlation between survival and the median date of autumn births described by Brockie *et al.* (1979). Survival of pouch young may well be higher, up to 100%, so the range of effective rate of births expected is given in each case (Table 4.8).

The assumptions made concerning the age of reproductive maturity, and the survival rate of pouch young, in calculating the effective birth rate in this manner mean that it is no more than an indication of the productivity of the populations. The contribution of spring births to the overall productivity has not been considered because of the sampling technique. However, it is expected that spring births occur in both the Middle Park and Kingston populations and possibly in the Poatina population as well. This expectation is because of the association between early median dates of autumn births and spring breeding (Brockie *et al.* 1979). The occurrence of spring births would raise the estimate of the effective

TABLE 4.8 Estimated range of effective birth rates for each of the four populations.

Locality	Net Natality	Expected Maximum Mortality (%)	Effective Birth Rate (Range)
Middle Park	0.39	10	0.35 - 0.39
Kingston	0.44	10	0.40 - 0.44
Poatina	0.47	10	0.42 - 0.47
Maggs Mt.	0.24	25	0.18 - 0.24

birth rate.

The annual rate of production of independent juveniles per adult is estimated for each population (Table 4.9). An adult is taken to be any individual two or more years of age. The annual rate of production of independent female juveniles is also calculated. Survival during pouch life is estimated to be above 90% at all but Maggs Mountain where it is estimated to be above 75% from Brockie's correlation.

The differences between the four habitats of the populations of Brushtail Possums examined here are reflected in the breeding performances of the populations. The two populations (Kingston and Middle Park) from woodland and pasture have early median dates of birth in the autumn breeding season and a lengthy period of breeding. The incidence of breeding in females is high although a bias towards male pouch young reduces the estimate of capacity of the populations to expand. It follows from the correlation between median date of birth and other breeding parameters noted by Brockie *et al.* (1979) that spring births would be expected, and would raise the estimates of the productivity of the population made here. The Poatina population is inhabiting a mosaic of open-forest and cleared land. This population shows a somewhat later median date for autumn births and consequently a shorter breeding season. The later median date of birth

TABLE 4.9 Estimated ranges of the annual production of independent juveniles per adult in each population.

Locality	Total Adults	Adult ♀♀	Adult ♀♀ with pouch young	Juveniles per adult	Adult ♀♀ with ♀ pouch young	♀ Juveniles per adult
Kingston	1.0	0.40	0.88	0.32 - 0.35	0.39	0.14 - 0.16
Middle Park	1.0	0.41	0.94	0.35 - 0.39	0.44	0.16 - 0.18
Poatina	1.0	0.52	0.82	0.38 - 0.43	0.47	0.22 - 0.24
Maggs Mt.	1.0	0.52	0.81	0.32 - 0.42	0.24	0.09 - 0.12

implies little spring breeding. There is a non-significant bias towards female births in this population which raises the value of net natality calculated and indications are that this population is the most productive of those investigated. It is estimated to produce more independent juveniles, particularly female juveniles, than any of the other three populations. By contrast, the Maggs Mountain population has a later median date of birth and a much shorter breeding season, so that spring births would not be expected here. This population demonstrates a much lower capacity to expand than do the other three examined. This population is living in habitat very similar to that of one of the populations examined by Hocking (1981) and exhibits similar characteristics.

4.5 SUMMARY

The breeding patterns and reproductive capacities of four distinct populations of Brushtail Possums have been examined. The characteristics displayed by each population fall within the range of those observed for other populations of this species.

The seasonal distribution of births is consistent with the findings of previous studies of *T. vulpecula*. Births occurred over a restricted period from late March to early June. The median date of births for populations in open woodland (Middle Park, 21 April; Kingston, 22 April) coincides with those reported for populations in similar habitat on mainland Australia (How 1972; Dunnet 1956; Smith *et al.* 1969). The median date of birth in the Poatina population from a forest pasture boundary is 30 April and the median date of birth in the Maggs Mountain population from regenerating tall-open forest later still on the 14 May.

An association between the length of the autumn breeding season and the median date of births was noted. The season ended at approximately

the same time in each population, so that those populations with earlier median dates of birth had a more extended breeding season.

The age at first breeding could not be determined using this sampling technique. It was assumed, therefore, that all females two years and over from each population were potentially capable of bearing young. The proportion of these females carrying pouch young was over 80% for all and in the Middle Park population was 94% (Table 4.9). The incidence of breeding in all populations of Brushtail Possums examined is generally high with more than 80% of females two years and over breeding each year (Brockie *et al.* 1979). The results of the present study are in accord with those of previous studies.

The estimated rate of production of independent juveniles varies considerably between the populations examined. This variation is attributed mainly to differences between the proportion of mature females in each population, and, where the production of female juveniles is considered, variations in the sex ratio of pouch young.

The reproductive capacity of the populations studied shows considerable variation and appears related to the habitat occupied, an association noted by Hocking (1981) for populations in southern Tasmania. He attributed this variation in breeding parameters to the quality of nutrition available.

CHAPTER 5 POPULATION STRUCTURE AND DYNAMICS

5.1 INTRODUCTION

Fluctuations in the size of a population are almost invariably associated with changes in population structure. Both result from changes in the pattern of recruitment and survival. This, in turn, is related to changes in the condition of the natural environment and to external factors such as hunting.

The purpose of this chapter is to examine trends in the patterns of recruitment and survival in the four possum populations. These trends are interpreted in terms of the hunting pressure the populations withstand and the environmental differences between the localities. This is done so that an evaluation of the effectiveness of this method in analysing trends in population dynamics can be made.

The population dynamics of possums have been considered in a number of studies. Several of them have examined the numerical response of the populations to some form of environmental fluctuation. Populations have been studied in relation to control operations using poison bait (Bamford 1972; Clout 1977), an eruptive fluctuation into previously unoccupied habitat (Boesma 1974; Fraser 1979), and successive stages of forest regeneration after fire (Hocking 1981). The results of this work have provided much information on the potential of the species to increase in various environments.

Other studies have looked at the dynamics of possum populations under stable conditions. These have been in both the native forests of mainland

Australia (Dunnet 1956, 1964; How 1972, 1981) and lowland New Zealand forest (Crawley 1973).

5.2 AGE STRUCTURE

All skulls were examined for molar wear and assigned to a molar wear class between 1 and 7 on the basis of the pattern of wear on the upper left molar, M^1, as described by Winter (1980). The distribution of skulls between molar wear classes has been given earlier (Table 3.4). Each molar wear class covers a narrow range of year classes. The distribution of known-age animals across each molar wear class (Table 5.1) was calculated from data in Winter.

TABLE 5.1 The proportional distribution of *T. vulpecula* from seven molar wear classes between year classes (data from Winter 1980).

	Molar Wear Class						
Age (in years)	M^1	M^2	M^3	M^4	M^5	M^6	M^7
0-1	0.48						
1-2	0.43	0.22					
2-3	0.09	0.62	0.63				
3-4		0.15	0.25	0.57	0.07		
4-5			0.13	0.29	0.35		
5-6				0.14	0.41	0.22	
6-7					0.18	0.39	0.20
7-8						0.28	0.60
8-9						0.11	0.20

Skulls in each molar wear class were allocated into year classes on the basis of this distribution (Table 5.2).

TABLE 5.2 Proportional allocation of *T. vulpecula* skulls into year classes on the basis of molar wear class.

		Age (in years)								
Location		0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9
Kingston	♂	4.32	8.49	32.10	22.14	13.83	9.97	6.45	4.32	1.59
	♀	2.4	5.67	19.82	13.83	9.63	7.48	4.32	2.92	1.04
	all	6.72	14.16	51.92	35.97	23.46	17.45	10.77	7.24	2.63
Middle Park	♂	1.44	6.35	30.28	15.61	7.20	3.51	2.30	1.72	0.64
	♀	0.48	2.19	16.39	10.82	7.46	4.62	2.03	0.88	0.31
	all	1.92	8.54	46.67	26.43	14.66	8.13	4.33	2.60	0.95
Poatina	♂	0.48	1.97	8.84	6.64	4.75	4.84	4.21	3.16	1.17
	♀	2.4	3.69	10.46	7.42	6.41	5.38	3.18	2.36	0.87
	all	2.88	5.66	19.30	14.06	11.16	10.22	7.39	5.52	1.99
Maggs Mt.	♂	0.00	0.44	3.13	2.33	1.67	1.10	0.36	0.00	0.00
	♀	0.00	0.66	3.75	1.91	1.38	0.96	0.56	0.60	0.20
	all	0.00	1.10	6.88	4.24	3.05	2.06	0.92	0.60	0.20

It is evident from Table 5.2 that possums between 2 and 3 years of age are the most numerous in each population. Possums less than 2 years of age make up only a small proportion of most samples. The sample from each population was collected by a professional shooter who was taking skins for trade. Skins from juveniles are not saleable because of their small size so juveniles are rarely shot. Young possums have more cryptic behaviour patterns than older animals (Dunnet 1956; Crawley 1973; How 1981) and are consequently less visible. Shooter preference for larger animals and the more cryptic behaviour patterns of younger animals are factors which cause possums less than 2 years old to be underrepresented in the sample.

These are generally transients, dispersing in the search for suitable habitat and not yet permanent members of a population. They are considered unlikely to make any effective contribution to the production of young. For these reasons possums in this age group were not incorporated into estimates of the structure and dynamics of the population. There is thus a hiatus between the time of independence and the time of recruitment into the resident populations. This hiatus was not examined. The two periods of life examined in this study are pouch life and estimates of the product-

ion of independent juveniles are made, and adult life where estimates of recruitment to the standing population and survival in adult age classes are made. Mortality in the intervening period is considered to be both high and variable and very much dependent upon the availability of unoccupied habitat to these dispersing individuals (How 1972).

In this study the rate of production of independent juveniles is estimated and compared with the rate of recruitment of subadults into the resident populations.

The number of possums in each age class declines steadily after the peak at 2 years in all populations. The rate of decline is different in each population. The estimated number of possums at each age is depicted in Figure 5.1. Losses due to death or emigration occurred at all ages in adult life but no distinction can be made between the two factors on the data available. Adult Brushtail Possums tend to be sedentary animals with a defined home range so emigration during adult life is considered to be unlikely to contribute much to the observed losses.

5.3 RECRUITMENT AND SURVIVAL OF ADULTS

Mortality is assumed to be the reason for the observed decline in numbers with age. The populations are subject to natural mortality and mortality imposed by hunting. Each area has the capacity to supply resources for living for a certain number of possums. Social and behavioural mechanisms operate to keep possums dispersed and to prevent increases in numbers above this level (2.2.3). Juvenile possums begin to disperse from their natal areas when they reach independence. How (1981) found that most of this movement occurs between 8 months and 2 years of age. Young possums are recruited into the resident populations by the time they reach 2 years. Hence, the peak of 2-year-olds in each population represents animals recruited to the population to replace losses due to mortality and, possibly, to increase the numbers in the population. Resident possums are territorial and dispersing individuals are only able to establish themselves in a

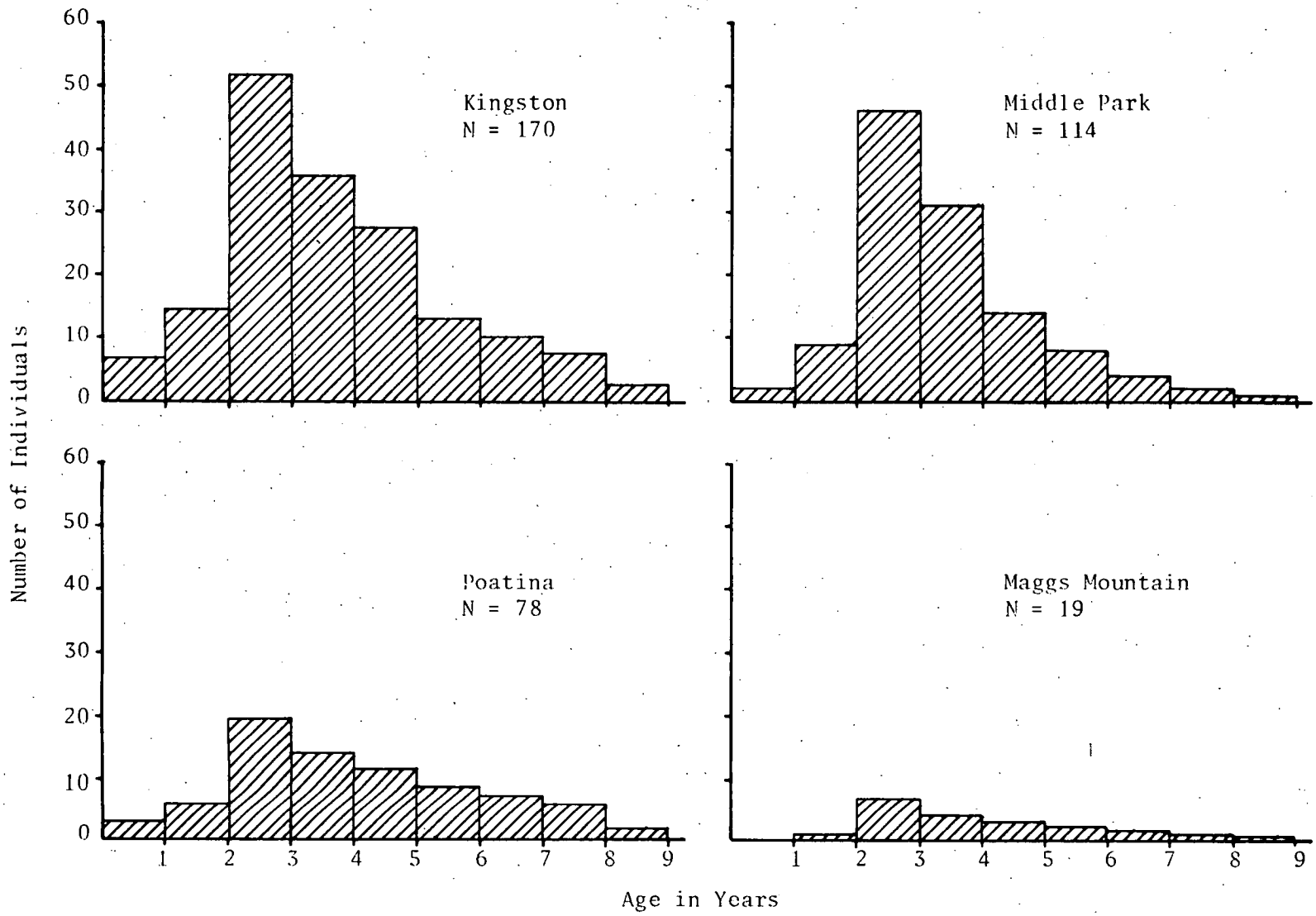


FIGURE 5.1 The distribution of possums into age classes for each of the four populations.

population where the habitat is not already fully occupied by resident animals. Juvenile Brushtail Possums are only able to establish themselves as residents within a population where there is suitable territory vacant. Thus the mortality of juveniles, and conversely, their rate of recruitment is related directly to the availability of unoccupied territory which will vary seasonally with adult mortality.

Each of the populations (with the exception of the Maggs Mountain population) came from localities where the land management regime had been consistent and unchanged for some decades. Populations from each locality have been hunted commercially over the same period, although the intensity of hunting has varied from year to year. The Maggs Mountain population is from an area which, as far as possums are concerned, has suffered a recent series of catastrophic events. Forestry coups on the plateau (Figure 3.5) have been clearfelled, burnt, and re-seeded between three and five years before this population was sampled. A control poison programme with 1080 baits was carried out in the regrowth areas the summer prior to sampling (1978/1979).

The secondary age ratio is the proportion of subadults in the population. It was determined from the ratio of the number of individuals aged two years to the total number of individuals aged two years and over for each population. Brushtail Possums two years of age are generally in their first breeding season (Smith *et al.* 1969; Hocking 1981) and are new residents of the local population, younger independent animals tending to be transients (Dunnet 1956; How 1981). This ratio thus gives a measure of the recruitment of new individuals to the population. There were marked differences in the values of the secondary age ratio between populations (Table 5.3).

Chi-square test gave significant differences between the middle Park and Poatina populations for the secondary age ratio ($P < 0.01$), there were no significant differences between the other populations.

TABLE 5.3 Secondary age ratio and estimated constant survival rate for four populations.

Locality	Secondary Age Ratio	Survival Rate (λ)
Kingston	0.35	0.65
Middle Park	0.45	0.55
Poatina	0.28	0.72
Maggs Mt.	0.38	0.62

Estimates of survival from one year to the next can be made from the age structure of the population if it is assumed that this age distribution is stable. Given the long term stability of the environment inhabited by three of the populations (Kingston, Middle Park, and Poatina) the assumption is justified in these cases. The age structure of the Maggs Mountain population is not expected to be stable.

A simple model of survival for individuals from age x years to age x + 1 years has been constructed using the secondary age ratio. It has been assumed that the age distribution for each population is stable, and that the survival rate λ is constant for adult age classes. If the number of individuals aged two years in the population is A, then the number of individuals aged three years is λA, four years $\lambda^2 A$, five years $\lambda^3 A$ and so on. Thus, $A + \lambda A + \lambda^2 A + \lambda^3 A + \lambda^4 A + \lambda^5 A + \lambda^6 A = \frac{A}{(1-\lambda)}$

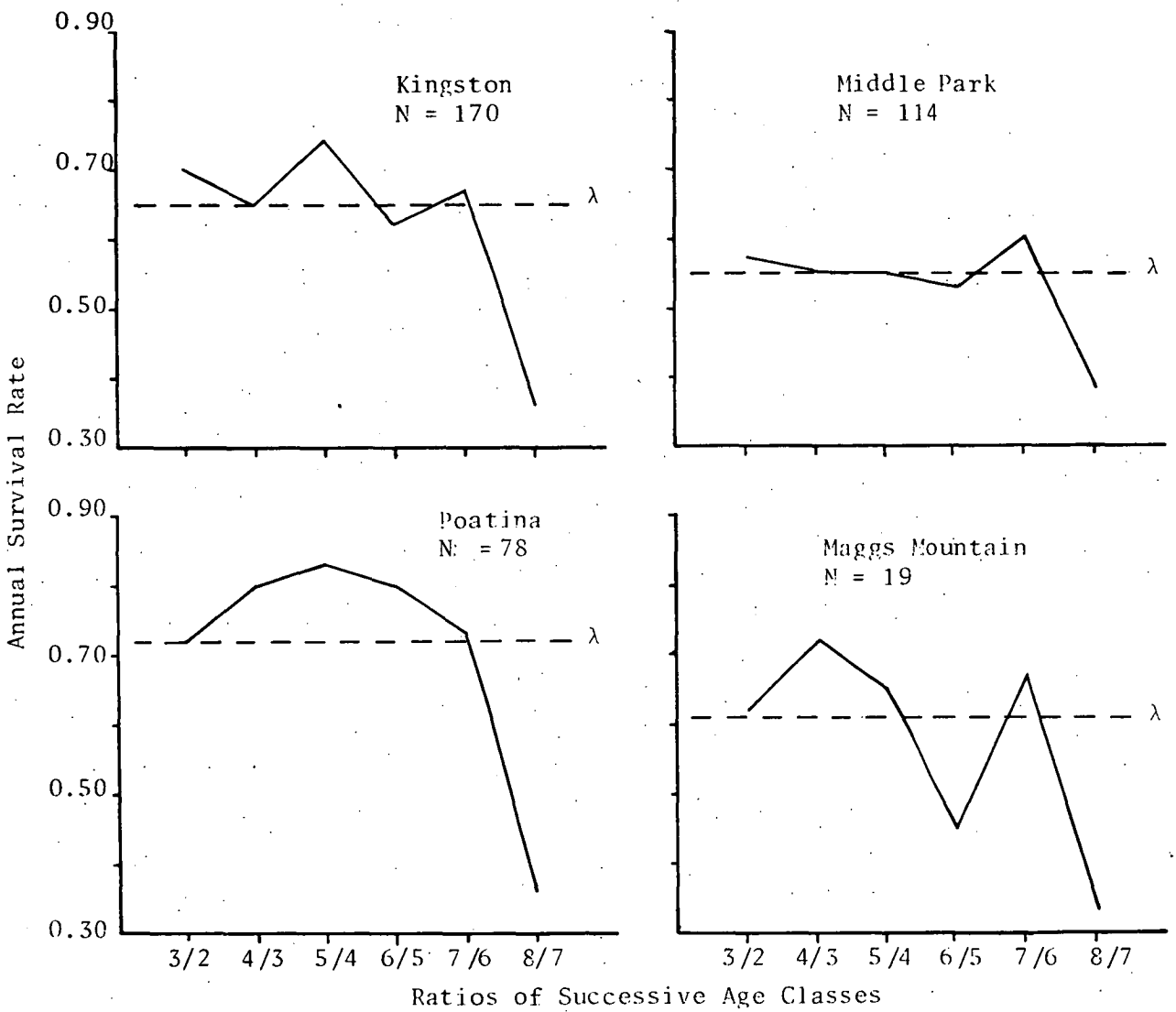
The secondary age ratio $= \frac{A}{A/(1-\lambda)} = 1 - \lambda$

hence $\lambda = 1$ - secondary age ratio (Table 5.3).

That this model approximates the real situation is shown by comparing the actual survival between successive year classes for each population (Figure 5.2).

The calculated survival rate, λ, approximates the observed pattern of survival between year classes for both the Kingston and Middle Park populations. Survival between year classes for adults in these populations is approximately constant. This is expected to be a consequence of hunting which is presumed to be the greatest cause of death and is non-selective among adults.

FIGURE 5.2 The proportion of individuals age x years surviving to age x + 1 years. The calculated constant rate of survival (λ) is shown.



The observed survival between successive age classes in the Poatina population is age dependent, increasing between the second and fifth years of life and declining at an increasing rate thereafter. Analysis of adult age structure in the Hokitika (New Zealand) population (Boesma 1974) suggested a high annual survival rate with a pattern of variation in survival similar to that of the Poatina population. Hocking (1981) found a similar age dependent survival pattern in populations from southern Tasmania.

The Maggs Mountain population was not expected to have a stable age distribution in view of the recent history of the site. It is interesting to note that survival between year classes 5 and 6 is very low. A large part of this area was recolonised after a regeneration burn at about this time. Brushtail Possums 6 years and older must be colonists, while those younger are recruited from juveniles born in the area supplemented, presumably, by immigration. The small sample size (N = 19) precludes any conclusions drawn from this observation.

Senescence and death due to old age appear to take effect in each of the populations after seven years (Figure 5.2). Survival between seven and eight years is between 30% and 40% in each of the populations, where it is above 60% between six and seven years for all.

It has been pointed out (Tyndale-Biscoe 1973) that hunting results in marked changes in the age structure of populations of *Trichosurus vulpecula*. The proportion of young animals in the population increases dramatically with increasing hunting mortality. The secondary age ratio is a measure of the level of recruitment of young animals to the population. The secondary age ratios found for these four hunted populations ranged between 0.28 and 0.45. Several unhunted populations in southern Tasmania showed secondary age ratios between 0.14 and 0.24 (Hocking 1981). The secondary age ratios for these populations were calculated in the same manner as those from the present study as a direct comparison between the

two is possible. Hocking's sample was collected in the course of a capture/release study, while these samples were collected by shooting so there may be some error due to the method of sampling.

All the populations in Hocking's study were pooled as were all the populations in this study. The difference between secondary age ratios for populations with high hunting mortality and populations with no hunting mortality was tested as follows.

It is assumed that the secondary age ratio is the same within each group.

θ_1 Hocking

θ_2 This study.

x_1	number of 2 year olds	Hocking	= 73.3
n_1	total adults	Hocking	= 354.0
x_2	number of 2 year olds	This study	= 124.8
n_2	total adults	This study	= 340.3

$$\text{if} \quad \frac{\frac{x_2}{n_2} - \frac{x_1}{n_1}}{\left[\hat{\theta}(1-\hat{\theta})\left(\frac{1}{n_1} + \frac{1}{n_2}\right)\right]^{\frac{1}{2}}} = Z \text{ with } N(0,1) \text{ tables}$$

$$\text{where } \theta = \frac{x_1 + x_2}{n_1 + n_2}$$

then $Z = 4.69$

= significance $P<0.0001$

The significance level strongly favours the secondary age ratio, and hence the recruitment rate, being much higher in hunted populations than in unhunted populations.

The annual recruitment rate required to replace losses due to mortality from all causes in the populations is the same as the secondary age ratio for stable, stationary populations which these are assumed to be. Comparison between the expected production of independent juveniles (Table 4.8) and

the level of recruitment needed to sustain the population at its present level gives a measure of the expected rate of increase (r) for each population (Table 5.4). This has been obtained by subtracting the number needed for recruitment to maintain the population from the estimated production of juveniles by the population.

TABLE 5.4 The expected rate of increase (r) for four populations.

Locality	$1 - \lambda^*$	# Juveniles**	Expected rate of increase
Kingston	0.35	0.32∿0.35	-0.03 ∿ -0.00
Middle Park	0.45	0.35∿0.39	-0.10 ∿ -0.06
Poatina	0.28	0.38∿0.44	+0.10 ∿ +0.16
Maggs Mt.	0.38	0.32∿0.42	-0.06 ∿ +0.04

*Secondary age ratio; ** Expected number of juveniles produced per adult member of the population

The Middle Park population shows a substantial negative rate of increase i.e. the population does not produce sufficient juveniles available for recruitment to maintain numbers at their present levels. The Kingston population shows a rate of increase about or just below zero, i.e. the population is producing barely enough juveniles to sustain itself. The Poatina population produces a large excess of juveniles and has the capacity to increase in numbers by up to 16% each year. The observed level of recruitment to the Poatina population is lower than for the other populations, and there is a surplus of juveniles which cannot be assimilated into their natal population. These individuals must disperse into unoccupied habitat or perish. The Maggs Mountain population has an expected rate of increase about zero. This figure must be treated with caution, however, as the age structure is assumed not to be stable and the sample size small.

The expected rate of increase as calculated is subject to two unquantified sources of error. These are juvenile mortality and the possible contribution of spring births to reproductive output.

Mortality among dispersing individuals is both high and variable. How (1972) considered this to be the most critical period of life with survival outside this period high. Studies on the social behaviour of possums (Winter 1976; Biggins and Oversheet 1978) suggest that mortality during this period is due, in a large part, to resident adults excluding juveniles from fully occupied territory. In these populations a high hunting mortality reduces the residents numbers leaving vacant territory available to these transients. Survival *per se* during this period of life has not been considered in this study but is expected to be high. It is treated as if it were 100% in each case.

The level of spring breeding has been correlated to the median date of autumn births (Brockie *et al.* 1979) and given the early median dates of birth in the Middle Park and Kingston populations there is the possibility that spring breeding contributes up to 15% of births. Under these circumstances the expected number of juveniles per adult member of the population would be as high as 0.40 for the Kingston population and as high as 0.45 for the Middle Park populations. With such high levels of spring breeding the rate of increase for the Kingston population would be positive (+0.01∿+0.05) and for the Middle Park population approaching zero (-0.04∿ 0.00). A comparison of the incidence of breeding in mature females for these populations (0.88 and 0.94 compared with 0.82) shows a higher proportion of females producing young.

The effect that the unquantified level of spring breeding and juvenile mortality have on the assessment of the dynamics of the population is discussed in Chapter 6 where the technique is evaluated.

A negative rate of increase in the populations is attributed to two factors:

(1) a high mortality rate due to severe hunting;

(2) the high level of hunting altering the population structure so that the proportion of reproductive females in the population is lowered.

Evidence has been presented earlier to support the first of these propositions, namely that survival between successive age classes is lowered in these populations and that the rate of recruitment of new individuals to the population is raised.

The second proposition, that hunting alters the sex ratio and lowers the proportion of reproductive females in the population is discussed.

5.4 DISPERSAL AND MIGRATION

Capture/release studies have demonstrated that adult possums of both sexes are sedentary (Hocking 1981) and rarely move more than 200 m from an established home range, always returning to it. Long-distance dispersal movements are characteristic of subadults, particularly males, and have been recorded in several studies (Dunnet 1956, 1964; How 1972; Clout 1977) of populations from various habitats. These dispersal movements were generally in excess of 1000 m and the animal did not return to its original range. The dispersing individuals were invariably young animals and usually immature (Dunnet 1956). Dispersal is seen to reflect the inability of the dispersing individuals to establish themselves in fully occupied habitat.

The social organisation of the Brushtail Possum has been studied (Winter 1976; Biggins and Overstreet 1978). The results of these studies support a relationship between survival and dispersal. Biggins and Overstreet (1978) found selective aggression by dominant males towards other males particularly juvenile males. This was not observed in females, and

these authors considered the socially mediated exclusion of juveniles to be predominantly an inter-male phenomenon. This is supported by finding that males have a greater tendency to disperse (Dunnet 1964; Clout 1977; Winter 1976) while some juvenile females establish ranges overlapping or adjacent to the maternal home range (Winter 1976).

Where a population produces a surplus of juveniles, social factors cause a migration of young out of the population, and these individuals are predominantly male. Thus, young possums recruited to a population in such circumstances, are more likely to be female. On the other hand, where there is a deficit of juveniles, those possums migrating into the population are more likely to be male.

The distribution between males and females in age classes is shown (Figure 5.3). In the Poatina population females predominate in the younger age groups, with the sex ratio approaching unity in older age groups. The Middle Park population shows an excess of males in the younger age groups, peaking at the age of recruitment (between 2 and 3 years), and approaching unity in older age groups. The Kingston population has an excess of males in all age classes. There was a slight predominance of females in the Maggs Mountain population.

Several studies have found significant variation in the sex ratios among different populations, with some populations showing a marked bias towards males. Clout (1977) found an excess of males among adults in a population inhabiting a young pine plantation, contrasting with the situation in an older adjacent plantation where females predominated. Fraser (1979) found an excess of adult males in a "moderate" density population while finding an excess of females in a nearby "high" density population. Hocking (1981) found an association between the age of the habitat (since firing) and the proportion of females, males predominating in younger habitats.

Clout (1977) attributed the observed differences in sex ratio to differences between the sexes in dispersal tendencies coupled with differ-

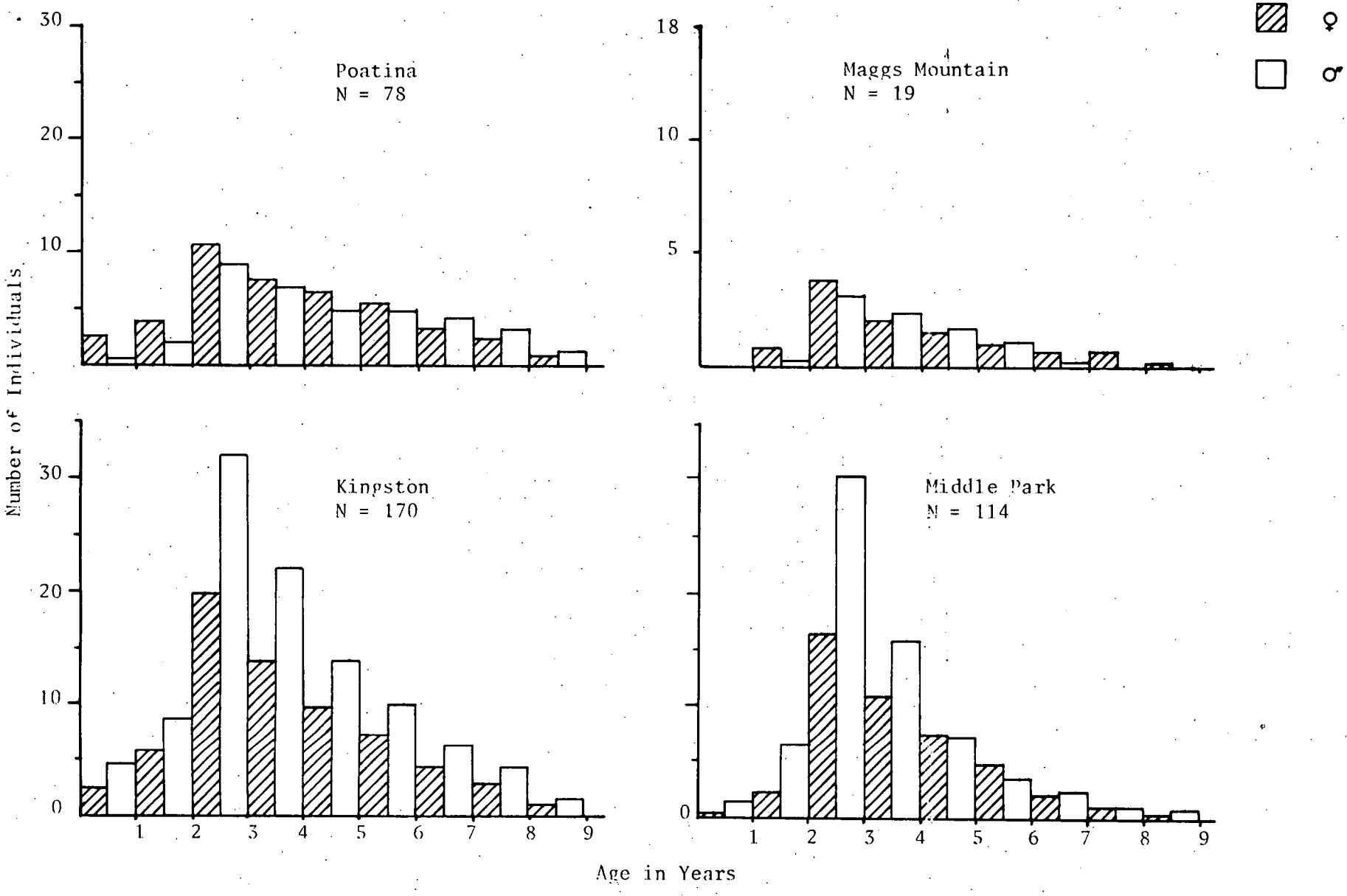


FIGURE 5.3 The distribution of males and females into year classes.

ences between the habitats. Males dispersed more widely than females and, consequently, were more likely to encounter and colonise vacant habitat. Where the habitat was more fully occupied, inter-male aggression prevented juvenile males establishing themselves.

The findings of the present study are consistent with this explanation. In the Kingston and Middle Park populations, the production of juveniles is not high enough to supply sufficient subadults to sustain the populations at their present levels. Consequently, there is vacant habitat available for colonisation and males are more likely to migrate into an area than females. In the Poatina population, the production of juveniles is in excess of the numbers needed to sustain the population, and inter-male aggression favours the recruitment of females to the population.

The level of hunting sustained by each population is presumed to account for the much higher recruitment rate of subadults found in these, as compared to un-hunted, populations. For the Kingston and Middle Park populations, the combined mortality due to natural causes and hunting is so high that the populations are sustained by immigration from surrounding areas. This immigration is predominantly male. Hunting mortality is presumed to be the main, proximal cause of death and to be unselective. Therefore, the selective immigration of males will cause an increasing trend towards males in the population. This is seen in a decline in the proportion of reproductively mature females with increasing long-term hunting pressure. The Poatina population has 46% adult females, the Middle Park population 37%, and the Kingston population 30%.

This demonstrates the effect that the level of hunting has on the reproductive capacity of the populations. Where the populations are unable to sustain their numbers without immigration, the predominantly male immigrants depress the proportion of reproductively mature females in the population.

5.5 SUMMARY

Comparison between the recruitment rates of subadults into resident populations of the Brushtail Possum shows that, in hunted populations, recruitment is significantly greater than in un-hunted populations. The secondary age ratio is used as a measure of the level of recruitment which, in a stable population, equates mortality.

Mortality in these populations is due to the combined effects of natural causes and hunting. The high rates of recruitment of subadults into these populations are presumed to be due to the high level of hunting mortality.

A comparison between the estimated production of juveniles and the observed recruitment rate for each population demonstrates that the Kingston and Middle Park populations are unable to sustain their present levels without immigration.

Immigrants into resident populations of the Brushtail Possum are predominantly male due to social factors mediating dispersal of juveniles. The disproportionate recruitment of males into the Kingston and Middle Park populations lowers the proportion of adult females in the populations thus reducing the population's capacity to produce juveniles.

Hunting alters the structure and dynamics of populations of Brushtail Possums. Where the level of hunting is greater than the population's capacity to sustain itself, social mechanisms operate to favour an increase of males in the population and further reduce the reproductive capacity of the population causing an accelerating decline.

CHAPTER 6 EVALUATION OF THE METHOD AND RESULTS FOR MANAGEMENT PURPOSES

The population biology of hunted populations of the Brushtail Possum *Trichosurus vulpecula* has been investigated with the view of developing a method of assessment that did not demand a large input of field time. The Brushtail Possum has considerable economic importance in Tasmania which is unique among Australian states in allowing commercial harvesting of the species. Under the *National Parks and Wildlife Act* (Tasmania) 1970, *T. vulpecula* is a partly protected species. The Tasmanian National Parks and Wildlife Service has the responsibility for maintaining a balance between conservation and exploitation of the possum.

As the level of hunting alters the population dynamics, it is necessary to monitor closely changes related to hunting. It is also important to monitor changes due to other factors such as habitat disturbance. The most rapid changes in land use in Tasmania at present are the clearing and regeneration of large areas of eucalypt forest in the production of woodchips for export. Brushtail Possums in these areas are subject both to changing patterns of land use and hunting pressure. The response of populations to these dual forces needs to be monitored so that future changes in the abundance and distribution of the species can be predicted. Manipulation of both can then be done to ensure that the status of the species in Tasmania is maintained at a desired level.

Efforts to monitor the species to achieve this objective have been hampered by a lack of suitable methods of population assessment. The Tasmanian National Parks and Wildlife Service carries out regular surveys

of the species to acquire the information needed. The methods give rather crude estimates of abundance and have been described as primitive by Frith (1979). These methods do not describe populations in terms of birth rates, recruitment rates or mortality so that estimates of the rate and direction of change in populations cannot be made.

The need for more sophisticated monitoring of populations of *T. vulpecula* in the state is recognised (Johnson 1977). Where human activities interfere with the dynamics of a species there is a need to predict the consequences of these activities. Levins (1970) has argued cogently that the primary goal of science is explanation to which the goal of prediction is subordinate. In the management of wildlife populations these priorities are reversed. The primary goal here is prediction.

A number of studies which describe and explain the population structure and dynamics of *T. vulpecula* have been made. The aim of this study is to provide a simple model of population structure and dynamics to facilitate prediction of response.

This was accomplished by using material salvaged from the possum harvest to estimate the rate of production of young, and the rate of recruitment of subadults to local populations. The difference between the two figures provides an indication of the rate and direction of any change in abundance of members of that population. A number of ancillary observations on breeding patterns, survival rates, sex ratios, and age structure of the populations supported the estimates made.

In any management oriented study, the time factor is of major consideration. Management authorities rarely have available the resources needed to conduct in-depth studies of the species for which they are responsible. They rely on relatively quick, relatively simple methods of assessment on which their evaluation of the likely response of a population to a given set of conditions is based. On the basis of these predictions, manipulations of the population to control this response to achieve a pre-determined aim

are made.

Survey methods can be broken down into the two main components. Sampling (or data collection) and analysis.

In this study the collection of the sample was delegated to a third party, commercial hunters. This division of labour offers distinct advantages to any management authority applying the method. The principal one is the saving of time; incidental benefits are the co-operation of hunters in maintaining their resource base, and the contact maintained between hunters and the management authority officers in the field.

It is important that hunters be reliable in the collection of the sample and that they be willing to co-operate. It is suggested that, where a survey of this type is carried out, the licence to hunt in the area only be issued on condition of co-operation. Also the licence should only be issued to experienced hunters who gain a large part of their income from this activity. These are people familiar with the species, who would collect a larger sample and possibly would be better motivated to co-operate fully as they would not wish to put future licences in jeopardy. Commercial hunters have a vested interest in maintaining their resource base. Good public relations by the management authority with, perhaps, some financial inducement such as a royalty should provide sufficient stimulus to guarantee co-operation.

The method of collection requires very little additional effort by the hunter. He lays aside the heads and pouch young from his harvest for collection by field officers of the department. Valuable information on the age at first breeding or reproductive maturity of females, together with information on age specific levels of breeding would be available if the association between the pouch young and the maternal skull were retained. This would required the tagging of each pouch young and associated skull. Where such information is felt to be necessary the pre-

preparation of suitable tags would minimise the time spent tagging in the field. Such tagging was not carried out on the sample used in this survey as there was no intention of analysing the collection for this purpose by the Queen Victoria Museum which arranged the collection.

A simple pattern of collection, measurement and analysis of material is set out below.

Step 1: Decision to sample a population to determine the observed rate of increase.

Step 2: The co-operation of an experienced hunter operating in the area is sought before the start of the season.

Step 3: The sampling technique is shown in detail to the hunter. Necessary equipment such as spikes to collect heads on, containers of formalin for pouch young, tags for skulls and pouch young. A collection schedule for the pick-up of material is arranged.

Step 4: Material is collected according to schedule, labelled and stored until the sample is complete.

Step 5: Measurements taken from the pouch young and date of birth estimated. Molar wear patterns of skulls examined and age at death estimated.

Step 6: Analysis of information. Estimates made of the rate of production of young, and the secondary age ratio to determine the observed rate of increase in the population.

Step 7: Examination of additional information such as sex ratios, survival between year classes, age at first breeding, median date of autumn births etc. can be made to give a more complete picture of the structure and dynamics of the population in question.

Age determination of adults and juveniles was made on the pattern of molar tooth wear, this is not the most accurate method available but is certainly the quickest. There is no preparation of the heads necessary, although workers may prefer to keep the heads deep frozen to minimise unpleasant odours. The distribution of the sample into year classes on the pattern of molar tooth wear is that described by Winter (1980). In this study, around four working days were taken to apportion the sample of 381 skulls examined into molar wear classes.

The proportional allocation of skulls into year classes on the basis of molar wear patterns requires a high degree of confidence in the reliability of the method. The data used to apportion wear patterns into year classes (Table 5.) is based on the wear patterns of animals of known age from a Queensland population. If this method of assessment were to be widely implemented to monitor Tasmanian populations of Brushtail Possums it would be advisable to make the correlation between molar wear patterns and cementum annuli. Adjustments could then be made so that the data used to apportion wear patterns into year groups would be from a local sample.

Age determination of pouch young was made by using the nomogram of Lyne and Verhagen (1957). These authors found a sigmoid pattern to their plotted observations but there were conspicuous deviations from fitting a single curve to the data. The growth curves could be satisfactorily described by fitting a parabolic function to the early part of the curve and an exponential function to the latter part. The authors presented their data in the form of a nomogram which has the value of being simple to use, applicable to a range of measurements of various body parts, flexible and easy to use in the field. The nomogram has been used in virtually every study of the species since 1957 to establish the age of pouch young. The accuracy of the data has been checked numerous times against pouch young of known age from various populations and found to be highly accurate.

Minor deviations from the plotted values have been found in advanced pouch young (more than 120 days) in some populations (Hocking 1981). There are no apparent advantages in converting the data to use regression analysis rather than the nomogram.

Recording the sex and estimated age in days of the sample of 397 pouch young took approximately five working days for two people, one handling the wet pouch young and taking measurements, the other recording.

These data were analysed to provide information on the breeding patterns and recruitment patterns prevailing in each population. From this estimates were made of the production of young and the recruitment of subadults into the population. The rate and direction of changes can be evaluated and the future status of the population predicted from this information.

The rate of increase (r) calculated (Table 5.4) is the actual capacity of the population to increase given the observed age structure and survival patterns of adult members of the population. It must be distinguished from the potential rate of increase (r_s) which is the population's potential to increase at a given rate in a given environment. This is an estimate of the rate at which the population would increase if it had a stable age distribution rather than the actual capacity to increase (r) which is influenced by whatever age distribution has been imposed on the population by previous events (Caughley and Birch 1970).

The calculation of r does not rely on any assumption of stability of age structure or population size, it is the expected rate of increase of a given population at a given point in time. Where the age structure of a population is stable then r is identical to r_s.

A number of breeding parameters were examined, including the incidence of breeding in females, the timing and distribution of births, and the sex ratio of pouch young. Several differences were noted between

the populations. The length of the autumn breeding season was apparently related to the median date of birth. Fecundity was generally rather lower than has been reported in other studies although of the same order as reported by Hocking (1981) for populations in southern Tasmania. The effective birth rate (the production of female young) showed greater variation between the populations, this being due to differences in the sex ratio of pouch young. A consistent bias towards male pouch young in *T. vulpecula* has been reported (Hope 1971), and this was found in the present study. The proportion of male pouch young appears habitat-related with a range of 0.44 male for Poatina to 0.76 in the Maggs Mountain population.

Brockie *et al.* (1979) reported an association between the median date of autumn births and a number of parameters of breeding performance. From these associations, the presence or absence of a spring breeding season, and the minimum survival rates of pouch young were inferred.

Estimates of the rate of production of independent juveniles per adult member were made for each population. No allowance was made for the possible contribution of spring births to the reproductive effort. Where these occur, the production of juveniles is underestimated. The effective birth rate was estimated to give an indication of the rate at which the populations could recover from a reduction in numbers if left undisturbed.

The level of spring breeding could not be determined from the data available in this study. Inferences drawn from the correlation noted (Brockie *et al.* 1979) between the median date of autumn births and the level of spring breeding imply that this could contribute up to 15% of the total reproductive effort of the Middle Park and Kingston populations.

Very few spring births (1%) were reported by Hocking (1981) in a study of Brushtail Possum populations in southern Tasmania. The median date of autumn births was later in these populations than in the Middle

Park and Kingston populations. It is recommended that before extensive use of this technique to monitor Tasmanian populations that samples be collected over the summer months to determine the presence and level of spring breeding in various habitat types. This would allow proportional adjustment to be made to the level of breeding calculated from winter collected samples.

The age structure and sex ratio of juveniles and adults from each population was examined. Survival between year classes for adults, and the secondary age ratio were calculated. The latter gives an estimate of the rate of recruitment of subadults into the population. Where the habitat is fully occupied the animals recruited are to make up losses resulting from hunting and natural mortality. Comparison between the rate of production of juveniles and the rate of recruitment of subadults to the populations allows prediction of changes in abundance.

The breeding patterns and the recruitment patterns are related both to the habitat occupied and the intensity of hunting. The recruitment level is closely bound to hunting intensity while the breeding pattern is more closely tied to the habitat occupied.

The survival of juveniles from weaning to recruitment was not estimated. Survival during this period is variable; where habitat is fully occupied social factors exclude juveniles so that survival during this period is directly related to the availability of vacant habitat. It is assumed, therefore, to be high where hunting pressure is high.

A number of inferences on the current status and probable direction of change in the populations were drawn from the analysis.

There is a highly significant difference between the rate of recruitment of subadults in hunted as compared with un-hunted populations. The high level of recruitment observed in the hunted populations is expected as a result of previously occupied habitat becoming available to new

recruits. Tyndale-Biscoe (1973) described the effects of hunting on the age structure of populations of *T. vulpecula*, the proportion of young animals being directly related to the measure of the intensity of hunting in a population.

A model of survival for adults was made (Section 5.3) and compared with observed survival between age classes. An examination of survival relies on either the actual survival of a single cohort over the life span of the species or for a population with a stable age structure the relationship between successive cohorts. Survival estimates made in this study were of the second type. The inherent assumption that the age structure of the populations was stable has been made.

This assumption cannot be justified from the data available which is from a sample taken in a single season. A later sample from these populations would provide direct evidence of the stability of the age structure. There are good reasons for assuming that the population size is fairly stable for three of the four populations, Maggs Mountain being the exception. These being that the populations are known to have been present and abundant for some decades under stable conditions of land management and a fairly sustained level of hunting. The level of hunting intensity cannot be quantified as no records are available. The only indication of hunting intensity available is local opinion which is that the numbers of Brushtail Possums taken from the areas is about the same from year to year.

The assumption that the population size is constant for Poatina, Kingston and Middle Park is justified on the grounds that little apparent change in habitat and the level of hunting has occurred for many years. Under such circumstances of stable conditions for several generations the local populations of Brushtail Possums could be expected to have a stable age structure.

The estimates of survival in adult life cannot be regarded as any more than indicators of general trends within the populations in the absence of data on the stability of the age structure of these populations.

Where hunting is less intense (as estimated from the secondary age ratio) the survival between year classes for adults is apparently age dependent (as in un-hunted populations) and the sex ratio of adults is close to unity. The Poatina population is an example of this situation. The recruitment rate is higher than in un-hunted populations, but the estimated production of juveniles is in excess of the numbers required to maintain the population.

Where the intensity of hunting is such that the population is unable to supply sufficient juveniles to maintain itself, a tip-over point is reached. Hunting, the main cause of death, is unselective with respect to age and sex, so survival between adult age classes is constant rather than age dependent. Residents are removed at a rate such that they cannot be replaced within the population and immigration becomes of major importance in maintaining numbers. Social factors governing the dispersal of juveniles mean that the bulk of the immigrants will be male. This lowers the proportion of females in the population and, hence, the capacity of the population to produce young.

This point has been reached in the Kingston and Middle Park populations. Survival between adult age classes is approximately constant, and near the value (λ) estimated from the rate of recruitment. This indicates that immigration is maintaining numbers at their current levels. This situation is inherently unstable as it relies on a continuing sufficient supply of immigrants from surrounding areas. As immigrants are predominantly male, the proportion of reproductively mature females is lowered, with consequent lowering of reproductive capacity and increasing the dependence of the population on immigration to sustain itself.

The status of the Maggs Mountain population is more difficult to evaluate. There have been major environmental disturbances within the life-span of members of the population; the oldest animals are certainly colonists. The sample size is small and, hence, random effects are large. Survival is neither constant between age classes nor wholly age dependent. There are indications that environmental perturbations affect survival. The population is predominantly male both for pouch young and adults. Hocking (1981) found the same tendency towards males in a similar habitat where the population was unaffected by hunting.

The analysis shows the status of the populations in some detail. Differences both in the production of juveniles and the survival of adults are readily apparent. The effects of hunting can be gauged. The results are compatible with those found in other studies of the species and in a form that allows comparison between populations samples in this manner and others where long-term studies have provided more detailed information.

The method of population assessment described here thus describes the current status of the populations and provides estimates of changes. It relies on the salvage of material from commercial hunters, laboratory examination of this material, and analysis of the results.

The introduction of this technique into the monitoring programme of the species carried out by the National Parks and Wildlife Service would involve preliminary work in determining the levels of spring breeding, and the relationship between molar wear patterns and year classes. The collection, measurement and analysis of the sample can be organised to provide detailed information on the status and dynamics of local populations of Brushtail Possums without the need for extended periods of field work.

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APPENDIX A: THE ESTIMATED DAY OF BIRTH FOR ALL POUCH YOUNG AT EACH LOCALITY

ESTIMATED DAY OF EACH BIRTH FROM THE KINGSTON POPULATION

Month	Day*	Males	Females	Total
	70			
	71			
	72		1	1
	73			
	74			
	75			
	76			
M	77			
A	78		1	1
R	79			
C	80			
H	81			
	82			
	83	1	1	2
	84			
	85	1		1
	86		1	1
	87			
	88			
	89			
	90		1	1
	91			
	92			
	93			
	94	1		1
	95			
	96	1	1	2
	97			
	98		1	1
	99	2	1	3
	100	1		1
	101	1	1	2
	102	1		1
	103	3	2	5
	104	3	2	5
	105	3	2	5
A	106	4	1	5
P	107			0
R	108	1	3	4
I	109	2	1	3
L	110		1	1
	111		3	3
	112		2	2
	113		1	1
	114	3	1	4
	115	1	1	2
	116	1		1
	117		1	1
	118	1	3	4
	119	2		2
	120		4	4
	121	2		2
	122		1	1
	123	1		1
	124	1		1
	125	1	1	2
	126			0
	127			0
	128			0
	129			0
	130			0
	131			0
	132	1	2	3
	133		1	1
	134	1		1
	135			0
	136			0
M	137	1		1
A	138			0
Y	139			0
	140	1	1	2
	141			0
	142		1	1
	143			0
	144		1	1
	145		1	1
	146			0
	147			0
	148	1		1
	149			0
	150			0
	151			0
	152			0
	153	2		2
	154			
	155			
	156			
	157			
	158			
	159			
	160			
J	161			
U	162			
N	163		2	2
E	164			
	165	1		1
	166			
	167			
	168		1	1
	169			
	170			

Month	Day*	Males	Females	Total
	171			
	172			
	173			
J	174			
U	175			
N	176			
E	177			
	178			
	179			
	180			
	181		1	1
	182			
	183			
	184			
	185			
	186	1		1
	187			
	188			
	189†			1
	190†			1
	191			
	192			
	193			
	194			
	195			
	196			
	197			
J	198			
U	199			
L	200			
Y	201			
	202			
	203			
	204			
	205			
	206			
	207	1		1
	208			
	209			
	210			
	211			
	212			

*Day is day of the year 1 January is Day 1 and 31 December is Day 356

†Unsexed newborn

ESTIMATED DAY OF EACH BIRTH FROM THE MIDDLE PARK POPULATION

Month	Day*	Males	Females	Total
	70			
	71			
	72	1		1
	73			
	74			
	75			
	76			
	77	1	1	2
	78			
	79			
M	80	1		1
A	81			
R	82	1		1
C	83	1		1
H	84		1	1
	85	1		1
	86		1	1
	87			
	88		3	3
	89		1	1
	90			
	91	1	1	2
	92	1		1
	93	2	3	5
	94	6		6
	95	1		1
	96	2	1	3
	97	1	5	6
	98	1	2	3
	99	5		5
	100	3	1	4
A	101	2		2
P	102	2	1	3
R	103			
I	104		1	1
L	105		1	1
	106	2	1	3
	107	2	3	5
	108	4		4
	109	1	3	4
	110	3		3
	111	1	1	2
	112	3	2	5
	113	5		5
	114	6	2	8
	115	1	2	3
	116	1	3	4
	117	1		1
	118	3	1	4
	119	1		1
	120	3	1	4
	121	2	1	3
	122	2	1	3
	123	1	1	2
	124	1	3	4
	125	1	1	2
	126			
	127		2	2
	128	2	1	3
	129			
	130			
M	131		1	1
A	132	2		2
Y	133		2	2
	134	1		1
	135		1	1
	136	1		1
	137		1	1
	138		1	1
	139		1	1
	140			
	141	1	1	2
	142		1	1
	143	1		1
	144	1		1
	145		1	1
	146	1		1
	147			
	148		2	2
	149			
	150	1		1
	151			
	152			
	153			
	154			
	155			
J	156		1	1
U	157			
N	158			
E	159			
	160		1	1
	161			
	162	1		1
	163			
	164		1	1
	165			
	166			
	167			
	168			
	169			
	170			

Month	Day*	Males	Females	Total
	171			
	172			
	173	1		1
	174			
	175			
	176			
	177			
	178			
	179			
	180			
	181			
	182			
	183			
	184			
	185	1		1
	186			
	187			
	188			
	189			
	190			
	191			
	192			
	193			
	194			
	195			
	196			
	197	1		1

Births detected outside the above period

Month	Day	Male	Female
JAN	20		1
FEB	40	1	
FEB	42	1	

*Day is day of the year 1 January is Day 1 and 31 December is Day 356

ESTIMATED DAY OF EACH BIRTH FROM THE MAGGS MOUNTAIN POPULATION

Month	Day*	Males	Females	Total
	70			
	71			
	72			
	73			
	74			
	75			
	76			
	77			
	78			
MARCH	79			
	80			
	81			
	82			
	83			
	84			
	85			
	86			
	87			
	88			
	89			
	90			
	91			
	92			
	93			
	94			
	95			
	96			
	97			
	98			
	99			
	100			
	101			
	102			
APRIL	103			
	104			
	105			
	106			
	107			
	108			
	109			
	110	1		1
	111			
	112			
	113			
	114			
	115			
	116			
	117			
	118			
	119	1	1	2
	120	1		1

Month	Day*	Males	Females	Total
	121			
	122			
	123	2		2
	124			
	125	1		1
	126	1	1	2
	127	2		2
	128	1		1
	129			
	130			
	131	1		1
MAY	132			
	133	1		1
	134			
	135	2		2
	136			
	137		1	1
	138			
	139			
	140	1		1
	141	2	1	3
	142			
	143			
	144			
	145			
	146			
	147			
	148		1	1
	149			
	150			
	151			
	152			
	153			
	154			
	155			
	156			
	157			
	158			
	159		1	1
	160	1		1
JUNE	161		1	1
	162			
	163			
	164			
	165			
	166			
	167			
	168			
	169			
	170			

Month	Day*	Males	Females	Total
	171	1		1
	172			
	173			
	174			
	175			
	176			
	177			
	178			
	179			
	180			
	181			
	182			
	183			
	184			
	185			
	186			
	187			
	188			
	189			
	190		1	1
	191			
	192			
	193			
	194			
	195			
	196			
	197			

*Day is day of the year 1 January is Day 1 and 31 December is Day 356

ESTIMATED DAY OF EACH BIRTH FROM THE POATINA POPULATION

Month	Day*	Males	Females	Total
	70			
	71			
	72			
	73			
	74			
	75			
	76			
	77			
M	78			
A	79			
R	80			
C	81			
H	82			
	83			
	84			
	85			
	86			
	87		1	1
	88			
	89			
	90			
	91		1	1
	92			
	93		1	1
	94			
	95			
	96			
	97			
	98		1	1
	99	1		1
	100		2	2
	101		2	2
	102			
A	103		1	1
P	104		1	1
R	105	3	3	6
I	106		1	1
L	107	1	1	2
	108	2	1	3
	109			
	110	1	7	8
	111		1	1
	112	1		1
	113	1	1	2
	114	3	1	4
	115	2	2	4
	116	3		3
	117			
	118			
	119	1	3	4
	120	2	2	4
	121	3	1	4
	122			
	123	1		1
	124		3	3
	125	2	1	3
	126	1	1	2
	127	2	1	3
	128	1	1	2
M	129	1		1
A	130	1	3	4
Y	131			
	132	2	2	4
	133	1	1	2
	134	1		1
	135			
	136	3	1	4
	137			
	138			
	139	1	1	2
	140	1	1	2
	141		2	2
	142			
	143			
	144	1	1	2
	145			
	146		1	1
	147			
	148			
	149		1	1
	150			
	151			
	152			
	153		1	1
	154			
	155			
	156			
	157			
J	158			
U	159	1		1
N	160		2	2
E	161	1		1
	162			
	163			
	164			
	165			
	166		1	1
	167			
	168		1	1
	169			
	170		1	1

Month	Day*	Males	Females	Total
	171			
	172			
	173			
	174			
	175			
	176			
	177			
	178			
	179		1	1
	180			
	181			
	182			
	183			
	184			
	185			
	186			
	187			
	188			
	189			
	190	1		1
	191			
	192			
	193			
	194			
	195			
	196			
	197			

*Day is day of the year 1 January is Day 1 and 31 December is Day 356